



Frequency dependent pollination for rewarding species in a combined approach of field data and agent-based modeling

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Abstract

Flower frequency dependence occurs if the frequencies in the flowering community affect the foraging behavior of pollinators. By influencing the plants fitness through differing visitation rates, frequency dependent pollination could have far-reaching consequences for plant coexistence. Negative frequency dependence, hence a pollinators preference for the rare species, is thought to enhance diversity and to be the reason for color morphisms in rewardless orchids. Common species on the other hand benefit from a positive frequency dependence which can reduce diversity. However, only few studies have been conducted on frequency dependence and are inconsistent with their results. Focus in this thesis is the analysis of frequency dependence for rewarding species in natural flower communities and the identification of influencing factors using a combined approach of field and model data.

I observed pollinator visitation to flowers of five rewarding species in their natural plant community in the area of the Jena Experiment. Thereupon I used an agent-based model of two co-flowering plant species competing over pollination service by a shared pollinator to identify patterns and influencing factors of frequency dependence.

Four out of five species showed a cubic frequency dependence in the field data. Furthermore, the results of the model support the general relationship and identify floral cover, cluster size and reward as important influencing factors. Negative frequency dependence was found for high floral cover, positive for low cover or very high reward.

In conclusion, my results indicate the existence of frequency dependent pollination for rewarding species in a natural flower community. Also, frequency dependence appears to depend on floral cover and spatial aggregation of flowers. Therefore, patterns of frequency dependence are likely to change in time and space and are not solely related to reward and certain species. In consequence, frequency dependence might be more important concept than previously thought for evolution and maintenance of diversity.

Keywords: Pollination, frequency dependency, flower constancy, foraging behavior, coexistence, agent-based model, density, patchy environment, nectar-production rates

1 Introduction

The majority of flowering plants species depend on pollination by insects for reproduction. Any advantage in attractiveness can be crucial for the plants fitness in the competition for pollination service of a shared pollinator. However, the foraging behavior is complex and influenced by various factors (Goulson, 1999). One pattern affecting the flower decision of pollinators is frequency dependence. Generally, frequency dependence of survival or reproduction is defined as relative fitness of a species as a function of its frequency in the community (Ayala and Campbell, 1974; Wright and Dobzhansky, 1946). In the case of plant-pollinator interactions, it occurs if the pollinator is influenced in its foraging behavior by the relative density of a species in a flowering community. Other species are neglected even if they are closer or more rewarding. Depending on their proportion in the flowering community, plants receive additional visits which can increase relative fitness and give an reproductive advantage due to increased seed set. According to ecological theory, frequency dependence can have far-ranging consequences for species coexistence and the maintenance of diversity (Levin, 1972). Two types of frequency dependence can be differentiated: Negative frequency dependence describes the preference of pollinators for the rare flower types which can result in a stable polymorphic equilibrium and an increase in floral diversity (Gigord et al., 2001). On the other hand, positive frequency dependence defines an advantage for the common phenotype which tends to reduce diversity in modeling studies (May 1974, but see Bever 1999, Molofsky and Bever 2002). For animal-pollinated plant species, optimal foraging theory predicts that under most circumstances pollinators should favor common flower types over rarer ones (Kunin and Iwasa, 1996).

While the positive effect of density dependence for pollination success is well studied (e.g. Essenberg 2012; Bernhardt et al. 2008; Kunin 1993; Morris et al. 2010), frequency dependence has rarely been tested. However, the few previous studies of frequency dependent pollination cover laboratory, field and modeling experiments.

In the review by Smithson (2001), 11 of 13 lab experiments using artificial flowers on a "bee-board" showed significant results for frequency dependence. 10 of those were done with rewarding flowers and resulted in positive frequency dependence favoring the abundant corolla color (Smithson and Macnair, 1996; Smithson and MacNair, 1997a). Negative frequency dependence was observed in the only experiment with non-rewarding flowers (Smithson and MacNair, 1997b).

Field experiments on frequency dependence were either wholly or partly manipulative and concentrated on color morphisms. Epperson and Clegg (1987) found the rare white morph of *Ipomoea purpurea* to be under-visited (but not the colored morphs) and Gigord et al. (2001) proved negative frequency dependent selection for the rewardless orchid *Dactylorhiza sambucina*, both supporting the lab experiments. However, Eckhart et al. (2006) was the first to prove negative frequency dependence for a rewarding species (*C. xantiana* ssp. *xantiana*) and to include natural frequencies. Other studies had no significant results (eg. Jones 1996; Mogford 1978) and experiments on natural flower communities have not been conducted yet to our knowledge.

While foraging models are relatively common, few investigate frequency dependence. The game-theoretic model by Kunin and Iwasa (1996) suggests pollinators should favor common flower types over rarer ones when resource availability is high. The similar mathematical model of Song and Feldman (2014) also concentrates on the pollinator perspective by applying rules of optimal foraging strategy to observe under which conditions the pollinators are able to maximize their net energy intake. Spatial explicit models grew in number over the last years addressing a range of foraging topics (Dornhaus et al., 2006; Bukovac et al., 2013; Faruq et al., 2013). Frequency dependent pollination is only subject to the model by Hanoteaux et al. (2013) who tested survival strategies for less attractive species over multiple generations.

In summary, previous research on frequency dependence is limited and inconsistent between lab, field and simulation data. Rewarding flowers are underrepresented in field and lab experiments and studies of natural flower communities lack completely. Furthermore, direct comparison of model and field data to cross-validate findings were only done for related questions such as density effects (Essenberg, 2012) and the learning abilities of bees (Dyer et al., 2014) but never for frequency dependence.

Furthermore, little is known of the influencing factors on frequency dependence which can be responsible for differing results of previous research. Smithson (2001) hypothesized in her review about factors including sampling size, floral traits and vision distance but did not test them. Density and spatial distribution of flowers can influence the perception of frequency of the pollinator and therefore also have interaction effects on frequency dependence.

While flower density is known to influence the foraging behavior of pollinators (eg. Kunin 1993; Essenberg 2012), a possible interaction with frequency dependence was not considered in most cases. Exceptions were Smithson and MacNair (1997a) who observed visitation rates for densities between 5 and 10% in their lab experiment without any significant result. Kunin and Iwasa (1996) and Song and Feldman (2014) included density as factor in their mathematical model and found it strongly influencing the optimal foraging strategy of pollinators.

In contrast to habitat fragmentation, the influence of spatial structure and distribution of flowers is not well studied although flowers typically exist in patchy distributions of various levels and sizes. Flowers are often clustered in inflorescences which are again clustered on the plant itself. Also individual flowers are likely to be aggregated in patches over the meadow. Usually, the proportion of flowers visited by pollinators declines with increasing cluster size, probably due to limited memory structure and the avoidance of previously visited flowers (Goulson, 2000). Geslin et al. (2014) found the foraging behavior of bumble bees (*Bombus terrestris*) affected by the spatial distribution of two co-flowering species in a controlled lab experiment. Again, the only study about spatial distribution of flowers in the context of frequency dependence was done by Hanoteaux et al. (2013). Within their model four levels of flower aggregation significantly influenced the survival rate of the less attractive species. The highest survival rates were found for big clusters in low frequencies and no clusters in high frequencies.

Given the general low quantity of studies concerning frequency dependent pollination and their inconsistent results, I want to address the following questions in this thesis:

1. Does frequency dependent pollinator foraging exist for rewarding species in natural floral communities?
2. What kind of a frequency dependent relationship can be found?
3. What are important factors influencing frequency dependence?

In a initial field study, I collected data on per-flower visitation rates of five different flowering rewarding plant species. Observations were made over a range of frequencies in their natural grassland plant communities in the area of the Jena Experiment. To understand which factors are influencing frequency dependence, I developed a spatially explicit model of two rewarding co-flowering plant species sharing pollination services. Agent-based models ("ABM", also known as individual-based models "IBM") are a valuable tool for assessing interactions in dynamic networks like financial markets, game theory, spread of diseases or, like in this case, ecosystems (DeAngelis and Mooij, 2005). The model contains multiple agents which behave independently after given behavior rules and are able to interact with the environment and each other. Agent-based models are especially suitable for analyzing behavior shifts with changing environmental conditions. In the model, frequency, floral cover and cluster size were included in the main analysis to broaden the knowledge gained by the exploratory field study. This approach makes it possible to identify subsequent research options to further evaluate frequency dependence.

2 Field Study

2.1 Methods

Study Site

The data used in this analysis were collected in the Jena Experiment, located north of the city of Jena in the center of Germany (N50°55' E11°35' ; 130 m a.s.l.) in July and August 2014. Mean annual temperature is 9.3°C and mean annual precipitation 578mm (Kluge et al., 2000). In 2002, 10ha of strongly fertilized arable field in a floodplain of the Saale river were converted into a biodiversity experiment. Species mixes of 1, 2, 4, 6, 8, 16 and 60 species from a pool of 60 common European grassland species were sown in 82 plots à 20m x 20m (Roscher et al., 2004). The Jena Experiment has the purpose to explore the effect of plant diversity (species richness and functional group richness) in grassland communities and is used in numerous studies and experiments.

The plots of the Jena Experiment are mowed twice a year in accord to standard grassland management. Parts of each plot are additionally weeded twice a year to maintain the original plant composition. Two subplots per plot were excluded from the weeding since 2002 ("Old Invasion Plots", 4m x 5.5m , 22m²) and since 2009 ("New Invasion Plots", 5m x 3.5m, 17.5m²) to evaluate invasive potential and effects. In 2014, subplots with continuous weeding were scarce with flowers and had a generally low species richness. Hence I collected the data in the old and new invasion plots with a higher cover, species richness and diversity. From the 82 plots of the Jena Experiment I only included plots with a floral cover between 20% and 70% for better comparability. In total, 23 plots were sampled throughout this study.

Data Collection

I selected the focal plant species during the field work as the flora changed very quickly and unpredictably. A focal species had to be flowering for at least one week in the sampling time and be present in at least five plots with a differing frequency to get sufficient data. Therefore, I chose *Lathyrus pratensis*, *Lotus corniculatus*, *Trifolium pratense* and *Onobrychis viciifolia* of the family Fabaceae and *Geranium pratense* of the family Geraniaceae (Supplementary material, tab. S1).

Pollinator observations were only made during suitable weather conditions (at most partly overcast, no more than light wind, min. 15°C). The sampling took place between 9am and 5pm. Overall, 15 days between 20th of July and 12th of August 2014 were suitable for pollinator observations. During each observation bout I recorded all pollinator activity during 15 minutes in a patch of 80cm x 80cm. This size is feasible to watch even with high pollinator activity and floral cover. The data collection included all visits to flowers of the focal plant species and total visitation number for all other flowers in the patch. I counted the flowers of the focal species to calculate the per-flower visitation rate. As possible drivers for visitation rate changes, I estimated the floral cover and identified all other flowering plant species present on patch and plot level. Each plot contained eight evenly distributed patches for 2h observation time per focal species and frequency.

Statistical Analysis

Per-flower visitation rate was used as response variable to identify frequency dependence. The number of visits per flower is an indication for the quantity of later seed set which again gives an advantage for reproduction and therefore the fitness of the species (Vázquez et al., 2005). In the analysis, per-flower visitation rate equals the count of visits of all pollinator types to all flowers of the focal species per patch within 15 minutes observation time divided through the number of flowers of the focal species within the patch. Therefore, the response variable is no count data and was modeled with a Gaussian error distribution in the analysis.

The explanatory variables of the full model were measured at plot level and included species richness, floral cover as single terms and frequency as single, quadratic and cubic term. Frequency (single and quadratic) was included in interaction with both floral cover and species richness as well as frequency (single, quadratic and cubic) and cover in interaction with species. Species was included as nominal response variable. All statistical analysis were performed with R, version 3.1.2. (R Core Team, 2014).

I used variance inflation factors (VIF) to check whether any variables in the dataset are collinear and should be removed prior to the analysis. With all values below two, there was no sign for collinearity and therefore acceptable to use them in the model selection as explanatory variables (Zuur et al. 2007, supplementary

material, Tab. S2). Pairwise scatterplots with included correlation of coefficients also showed only minor correlation (Supplementary material, Fig. S2).

The sampling design contained 8 observations per plot summing up to 2h of observations per species and frequency. Therefore, the data are not independent and I chose a linear mixed effect model with subplot nested in plot as random effect. I used the function "lme" from the R package "nlme" (Pinheiro et al., 2014) for all further analysis.

The full model with all predictors and interactions showed a strong pattern of heteroscedasticity in the residuals. With the varIdent-function from the R-package "nlme", every species is allowed to have its own variance structure and we can maintain the differences in attractiveness of the five focal species in the model as biological information. The weighting provided a significantly better variance structure for the model ($L = 383.74$, $df = 4$, $p < 0.0001$).

I performed a backward stepwise deletion of interactions and predictors with maximum likelihood estimation for each model. The loss of explanatory power in the model after removal of a variable was tested by comparing the Akaike information criterion (AIC) of the model with and without the explanatory variable (ANOVA model comparison). If there was no significant loss of explanatory power, the variable was removed. The selection was verified by a global selection via the dredge-function from the R-package "MuMin" (Barton, 2014) with maximum likelihood estimation.

The final model was again validated by plotting the normalized residuals against fitted values. The vertical gap in the residuals can be explained by the difference in flower attractiveness (Supplementary material Fig. S3). *Geranium pratense* and *Onobrychis viciifolia* received very high visitation rates whereas *Trifolium pratense*, *Lotus corniculatus* and *Lathyrus pratensis* had generally only few visits. However, the heteroscedasticity of residuals could be dealt with by the weighting and the mean of the residuals is close to zero (< 0.0001).

2.2 Results

Visitation Rates

In total, I made 385 observations, each representing pollinator activity records for 15min in a 80cm x 80cm patch representing 96,25h of observation on 246.4m².

Onobrychis viciifolia was the most attractive plant with a maximum of 318 visits in one observation. The per-flower visitation rate varied strongly with the attractiveness of the focal species. Per observation, I recorded 1.4 ± 1.8 (mean \pm SD) visits per flower with a maximum of 10.7 visits per flower (again *Onobrychis viciifolia*) and 31 observation with no visit at all to the focal species. The per-flower visitation rate was significantly different between the two very attractive species *Geranium pratense* and *Onobrychis viciifolia* and the three less attractive species *Trifolium pratense*, *Lotus corniculatus* and *Lathyrus pratensis* ($P \leq 0.001$, Tab. 1). The subplots contained 3 ± 1.2 (mean \pm SD) flowering species including the focal species, the species richness was higher at the plot level with 8 ± 2.4 (mean \pm SD) flowering species.

Table 1: Per-flower visitation rates (mean \pm SD) for the focal flower species per 15 minute observation. *Geranium pratense* and *Onobrychis viciifolia* are significantly different from the other three species (pairwise t-test, $p < 0.001$). Within the two groups, there is no significant difference between the species.

Short	Species	Family	Visitation Rate (Mean)	SD
Ger	<i>Geranium pratense</i>	Geraniaceae	3.05	1.5
Lat	<i>Lathyrus pratensis</i>	Fabaceae	0.57	0.53
Lot	<i>Lotus corniculatus</i>	Fabaceae	0.30	0.36
Ono	<i>Onobrychis viciifolia</i>	Fabaceae	3.60	2.5
TP	<i>Trifolium pratense</i>	Fabaceae	0.16	0.23

Frequency Dependence

Floral cover and species richness had both individually and in the interaction term with frequency no effect on the visitation rate and were removed from the model (Cover: $F_{df=1} = 1.17$, $P = 0.28$; Species Richness: $F_{df=1} = 1.15$, $P = 0.29$).

The linear mixed effect model showed an effect of species and frequency individually and with interactions on the per-flower visitation rate (Species: $F_{df=4} = 141.13$, $P \leq 0.0001$; Frequency: $F_{df=1} = 18.29$, $P \leq 0.0001$; Species x Frequency $F_{df=4} = 5.2$, $P \leq 0.001$, Tab. 2). Interestingly, frequency contributed also as quadratic and cubic term with its interactions to species explanatory power to the model, giving the relationship a non-linear character. Figure 1 shows a cubic relationship of four focal species and the summed data and a quadratic relationship for *Lathyrus pratensis*. The cubic curve is defined by a strong increase for frequencies below 20% followed by a minimum between 50 and 80% depending on the species before raising again with increasing dominance of the focal species. However, the visitation rate of *Lathyrus pratensis* showed a maximum at 60% frequency and decreases afterwards.

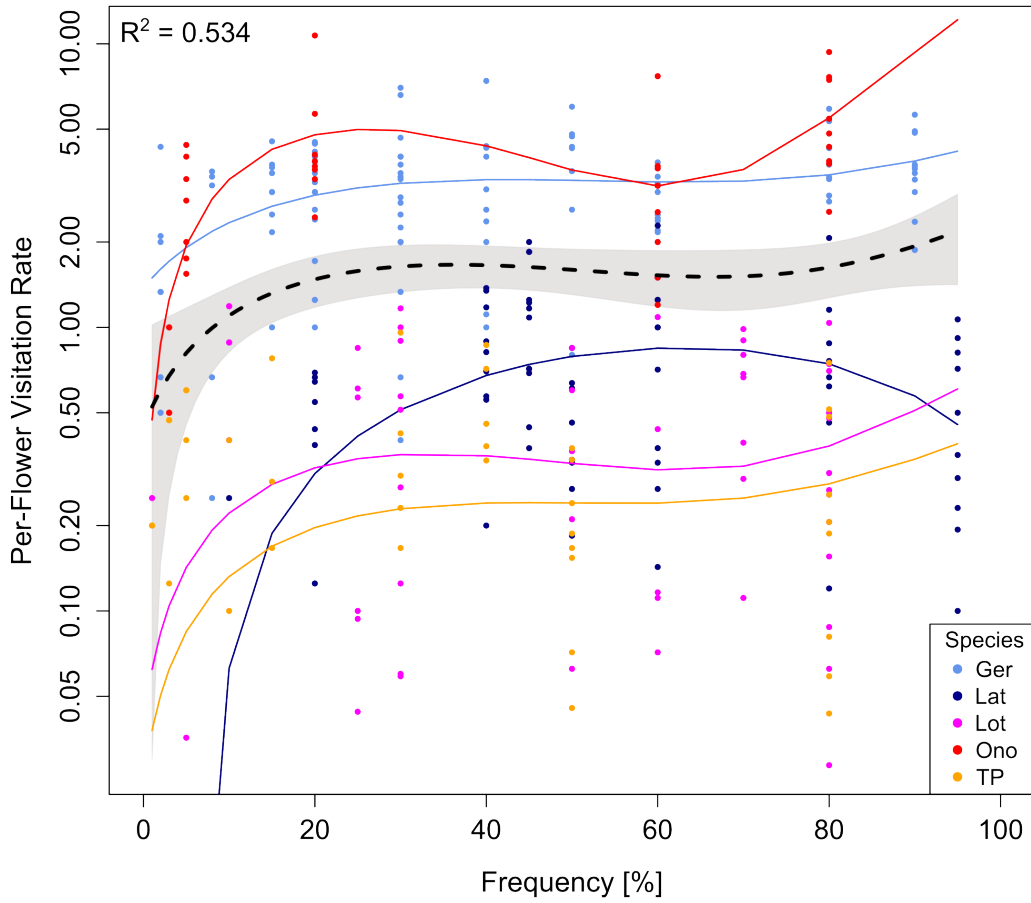


Figure 1: Relationship between per-flower visitation rate and frequency for the five focal species. Each point represents one observation of 15 minutes. The y-axis is plotted on a log scale due to the wide variance in attractiveness between the focal species. The model shows a cubic frequency dependence for all species but *Lathyrus pratensis*. The dashed line represents the prediction for the overall model with its 95% confidence-interval (grey area). Floral cover and species richness were dropped as explanatory variables in the model selection process. R^2 was calculated with the "r.squaredGLMM"-function of the MuMIn-Package (Barton, 2014)

Table 2: Results of the linear mixed effect model with per-flower visitation rate as response variable. Floral cover and species richness and its interactions with frequency were removed in the model selection process (denDF = 191, $R^2 = 0.53$, $n = 385$)

Explanatory Variables	Df	F-value	<i>P</i>
Frequency	1	49.3	< 0.0001
Frequency ²	1	13.2	0.0026
Frequency ³	1	5.8	0.8145
Frequency x Species	4	5.2	0.0005
Frequency ² x Species	4	3.4	0.0097
Frequency ³ x Species	4	3.4	0.0101

3 Agent-Based Foraging Model

3.1 Methods

Main Features

The model was developed on the basis of empirical findings for foraging rules and pollinator behavior. It is a simple spatial model of two co-flowering plant species competing over pollination service.

In the model, all pollinators (from now on called "bee-agents") are identical and the two flower types only differ in their species identity. Reward replenishment, handling times to extract the reward and its attractiveness towards the bee-agents is identical for both species. Corolla color is only assigned for better visualization and is meaningless for the model or the bee-agents, respectively. All bee-agents behave under the hypothesis of flower constancy which is empirically tested for various pollinators (e.g. Hill et al. (1997) for honey bees, Chittka et al. (1997) for bumble bees, Goulson and Wright (1998) for hoverflies and Goulson et al. (1997) for the butterfly *Thymelicus flavus*). Flower constancy is the tendency of an individual pollinator to keep visiting the same flower species instead of switching to more rewarding or closer species (Chittka et al., 1999; Waser, 1986). Because we are interested in the visitation rate of flowers in different frequencies, the energetic costs and the limit of gained rewards of the bee-agents are ignored. Furthermore, they do not communicate and always empty a flower completely.

Model Environment

I used NetLogo (Wilensky, 1999) as programming environment. It is a simple but powerful tool for making agent-based models and connectible with R through the R-package "RNetLogo" (Thiele et al., 2012). In NetLogo, the "world" is a spatial grid with a set number of cells called patches. Agents can move freely over the patches according to their given behavior rules. Patches and agents both have own properties and can interact with each other. In my model, the "meadow" has 100x100 grid cells with horizontally and vertically wrapping to avoid edge effects. Every grid cell can either contain a single flower of one of the two species or grass.

Figure 2 shows a set of exemplary model environments. Floral cover is defined as the percentage of the patches containing flowers and the cluster number equals the average number of flowers within a cluster. The number of clusters per species is calculated by dividing the number of flowers per species on the meadow through the cluster number. If the cluster number is one, all flowers are randomly distributed over the meadow. With increasing cluster size, one flower per cluster is initially assigned on the meadow ("cluster-seed") and all remaining flowers of that species are randomly allocated to them in a second step.

Every flower contains 1 Joule of reward in the beginning of each simulation run. The bee-agents are randomly distributed over the modeling environment and start without a fixed preference for a flower type but just pick the closest one when the simulation starts. Every time step in NetLogo equals one second.

Behavior Rules

All bee-agents act independently from each other according to the behavior rules shown in Figure 3 (Overview of all parameters used for the model with its default settings in the supplementary material in Tab. S4).

As mentioned in the assumptions, the behavior of the bee-agents is strongly influenced by flower constancy (e.g. Bobisud and Neuhaus, 1975; Chittka et al., 1997; Thomson, 1981; Chittka et al., 1999; Goulson, 1994, 1999). Bee-agents always prefer one of the two flowering species and forage exclusively on this species. The preference can change due to lack of searching success or a series of low rewards of the preferred flower (Chittka et al., 1997; Kunin, 1993; Greggers and Menzel, 1993). At any given time, a bee-agent can be in one of two states: search for a flower or visit one.

Search

Pollinators avoid recently visited flowers (Goulson, 1999). Every bee-agent possesses a memory to remember the location of the last four already visited flowers (Goulson, 2000). If there is any not recently visited and preferred flower in sight, the searching bee-agent moves directly towards the flower, otherwise it continues searching.

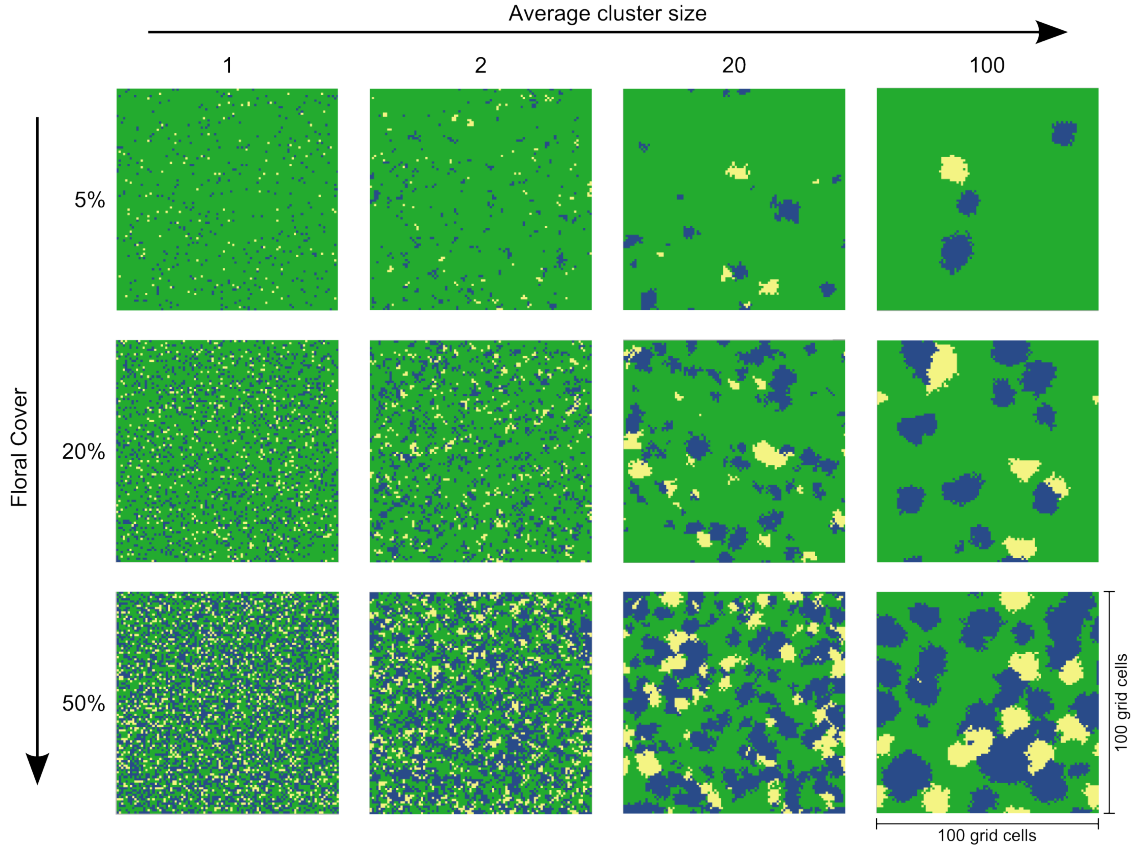


Figure 2: Exemplary model environment setups with increasing floral cover and cluster size. The cover expresses the percentage of patches containing a flower ($N_{patches} = 10\,000$). The cluster number equals the average amount of flowers per cluster. Green patches represent grass, yellow and blue patches are flowers of species A (25% frequency) and B (75% frequency). Flowers are randomly assigned to the clusters in the model setup.

Previous research on the speed of foraging pollinators by Essenberg (2012) and Kunin (1991) gives 0.1m/sec as benchmark. Consequently, bee-agents can move 1 grid cell per time step in this model. The vision of pollinators was studied in various experiments using a Y-maze apparatus (Dyer et al., 2008; Wertlen et al., 2008; Ne’eman and Kevan, 2001). Every bee-agent can detect flowers from a distance of 0.7m with an equivalent of 6 grid cells. The vision is reduced to a 180° cone-shaped field to the front of the agent. Pollinators tend to keep their direction while foraging (Waddington, 1980). In the model, I used a correlated random walk (CRW) to achieve a relatively natural movement (Bartumeus et al., 2005; Codling et al., 2008; Pyke and Cartar, 1992; Viswanathan et al., 2008). Empirical studies have shown an increasing probability to abandon the original flower preference the longer the search remains unsuccessful (Chittka et al., 1997; Kunin, 1993). If the bee-agent searches for 5 seconds (= 5 time steps) without finding any preferred and unvisited flower, the likelihood of changing its preference increases by 10% with every additional time step.

Visit and Reward Intake

When a bee-agent encounters a preferred and unvisited flower it takes up all its reward. As long as the reward content of a flower is lower than the maximum it is refilled by 0.00004 Joule in each time step until the maximum of 1 Joule is reached (see "reward-function" in Tab. S4). The handling time of a bee-agent visiting a flower involves three components: a time proportional to the amount of reward taken, a reward-independent constant and a skill factor (Kunin and Iwasa, 1996). In my model, a bee-agent requires 4 seconds to extract one Joule of reward plus a reward-independent handling time of 0.5 seconds. When the bee-agent just changed its flower preference it gets a 3 second penalty for inexperience (Roubik 1992, Kunin and Iwasa 1996).

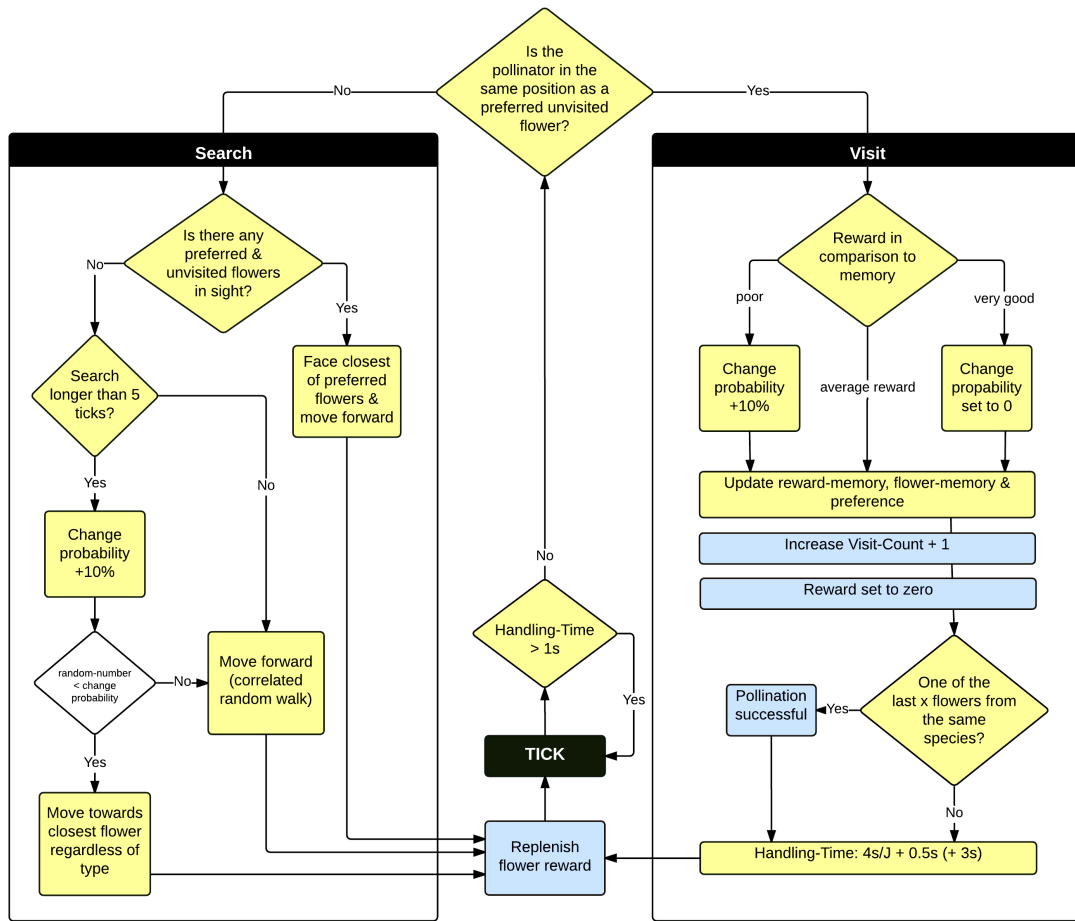


Figure 3: Flowchart describing the behavior rules for the bee-agents within the agent-based model. At any time given, a bee-agent can either search for a preferred flower or visit one. While searching, a bee-agent can remember the location of the last four visited flowers to avoid double-encountering. If there is no flower in sight after 5 seconds of correlated random walk (CRW), the probability that it will encounter the next available flower regardless of species increases by 10% per additional time step. When a bee-agent visits a flower it takes all reward within a reward-dependent handling time and compares the amount with its memory. If the reward is low, compared to the average of the last 4 visits, the agent is more likely to visit the other flower type next time. The maximum of visits within a successful pollination is determined by the pollen carryover parameter. In the main analysis, values for pollen carryover lay between 1 and 16 heterospecific visits (see Tab. 3)

The reward taken is stored in each individual's reward-memory. Every bee-agent can remember the last four rewards received. When visiting a flower, the bee-agent compares this memory with the current reward quantity. If the reward is less than half the average in the memory, the likelihood to abandon flower constancy and visit the other species next increases by 10%. If the reward is exceptionally good (at least twice the remembered average), the change probability is set to zero (Chittka et al., 1997; Keasar et al., 1996).

Additional to the quantity of visits we're also interested in their quality. A flower can only be successfully pollinated if the bee-agent visited the same species before. The maximal number of heterospecific flower visits which still allows successful pollination is determined by the degree of pollen carryover. The parameter applies to all bee-agents and can have a value between 1 and 16. For the value of one, the very last visit has to be from the same species (strong heterospecific pollen interference, see Campbell 1986; Benadi et al. 2012; Montgomery 2009).

After reward-collection is completed, the bee-agent updates its flower-memory and its reward-memory and

continues foraging. Each visit and successful pollination is recorded for later analysis.

Simulation Experiments

Parameters altered in the main analysis are frequency, floral cover, degree of clustering and pollen-carryover. Each parameter-combination was run 20 times with a length of 1000 ticks each (110,400 runs in total). Additionally, I performed a sensitivity analysis with parameters affecting the behavior of the bee-agents to understand how the values of these parameters influence the frequency dependence of per-flower visitation rate. Table 3 presents the definition and value range of the parameters.

Table 3: Parameter values used for the main and sensitivity analysis. Only general parameters were changed in the main analysis, whereas the sensitivity analysis also directly influences the behavior of the bee-agents. Each combination was repeated 20 times for 1000 time steps, that makes a total of 110,400 runs in the main analysis and 16,560 runs for each parameter of the sensitivity analysis.

Parameter	Description	Values
MAIN ANALYSIS		
Frequency	Proportion of species A on all flowers	0-100% (5%-steps)
Flower cover	Proportion of patches containing a flower	5, 10, 20, 50 %
Degree of clustering	Average number of flowers per cluster	1, 2, 5, 10, 20, 50, 75, 100
Pollen carryover	Number of visits within a successful pollination is possible	1, 2, 4, 6, 8, 16
SENSITIVITY ANALYSIS		
Reward function	Increase of reward per flower and second	0, 0.00004, 0.001, 0.1 J/sec
Vision distance	Range of patches within a bee-agent can detect flowers	1, 6, 20, 50 patches
Search time	Number of seconds a bee-agent searches before the probability of switching flowers increases	1, 5, 20, 50 sec
Pollinator density	Number of bee-agents on the meadow	5, 10, 20, 50 bees

3.2 Results

Per-flower Visitation Rate

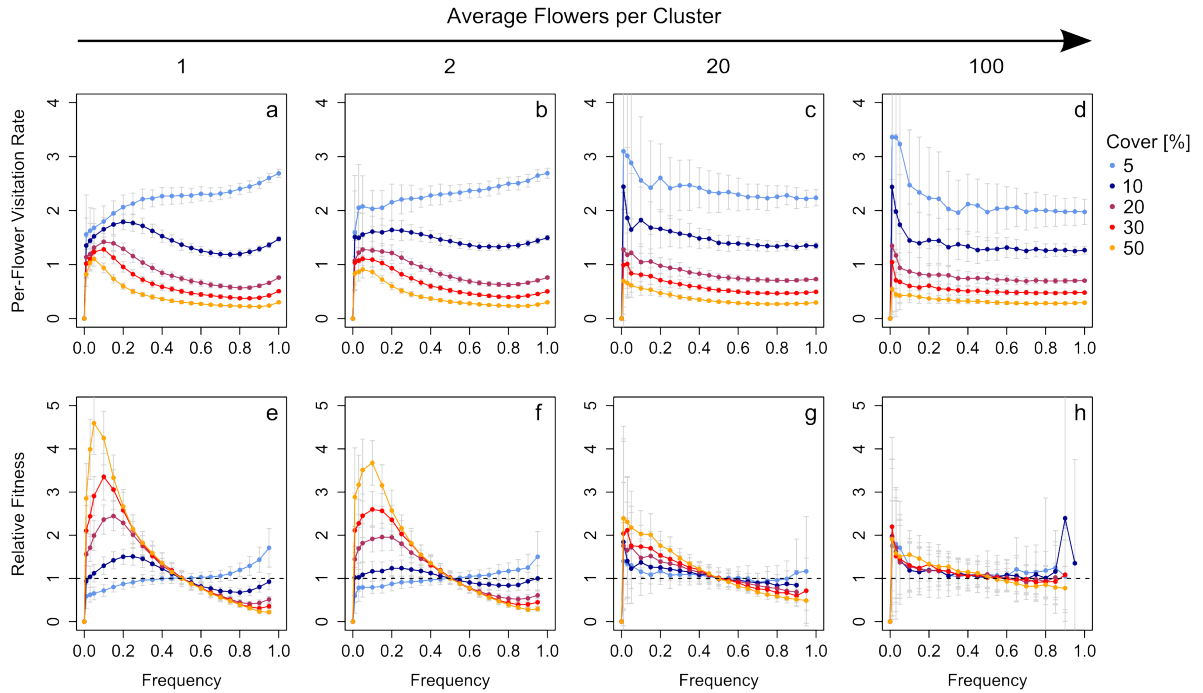


Figure 4: The per-flower visitation rate shows a frequency dependence with a cubic relationship. The same data is plotted relative to per-flower visitation of the other species to visualize the relative fitness and intensity of frequency dependence (e-h). A value of one means no benefit in visits per flower for either species. The frequency effect is stronger for higher floral cover while an increase in cluster size reduces the frequency dependence. The peak at 90% for 10% cover in a 100 flowers per cluster environment is due to a statistical outlier highly influencing the mean. The parameter combination was run again for validation (supplementary material, Fig. S11). Note that the statistical variability increases for very low frequencies in highly clustered scenarios (grey error bars). If a rare species is occurring only in one cluster on the meadow, it will receive either no or multiple visits. See Fig. S10 in the supplementary material for an enlarged image.

The per-flower visitation shows for small clusters a similar cubic function as the data collected in the Jena Experiment (Fig. 4a,b). Within the first 20% there is a steep increase in visits per flower. Afterwards, since for all cover values above 5% the additional gain of visits is not proportional to the increase of flowers due to higher frequency, the per-flower visitation drops with a minimum around 80%. Close to 100%, when the species becomes dominant, the per-flower visitation rises again. Cover and cluster size both influence the frequency dependence. The higher the cover, the lower the per-flower visitation and the bigger the clusters the less visible is the frequency dependence. Simulations with more than 10 flowers per cluster show a high variance for frequencies below 10% and very low to no frequency dependence afterwards (Fig. 4c,d).

The same data is plotted as relative visitation rate to see which species has a higher fitness and to take the variance in the sum of visits into account (Fig. 4e-h; see section "Global visitation"). If the value is one, both species receive the same per-flower visitation. For 5% cover, the bee-agent exhibits a positive frequency dependence. If the cover is higher, the rare species benefits from a negative frequency dependence. Cluster size reduces the effect and the data approach a slightly negative frequency dependence (Fig. 4h).

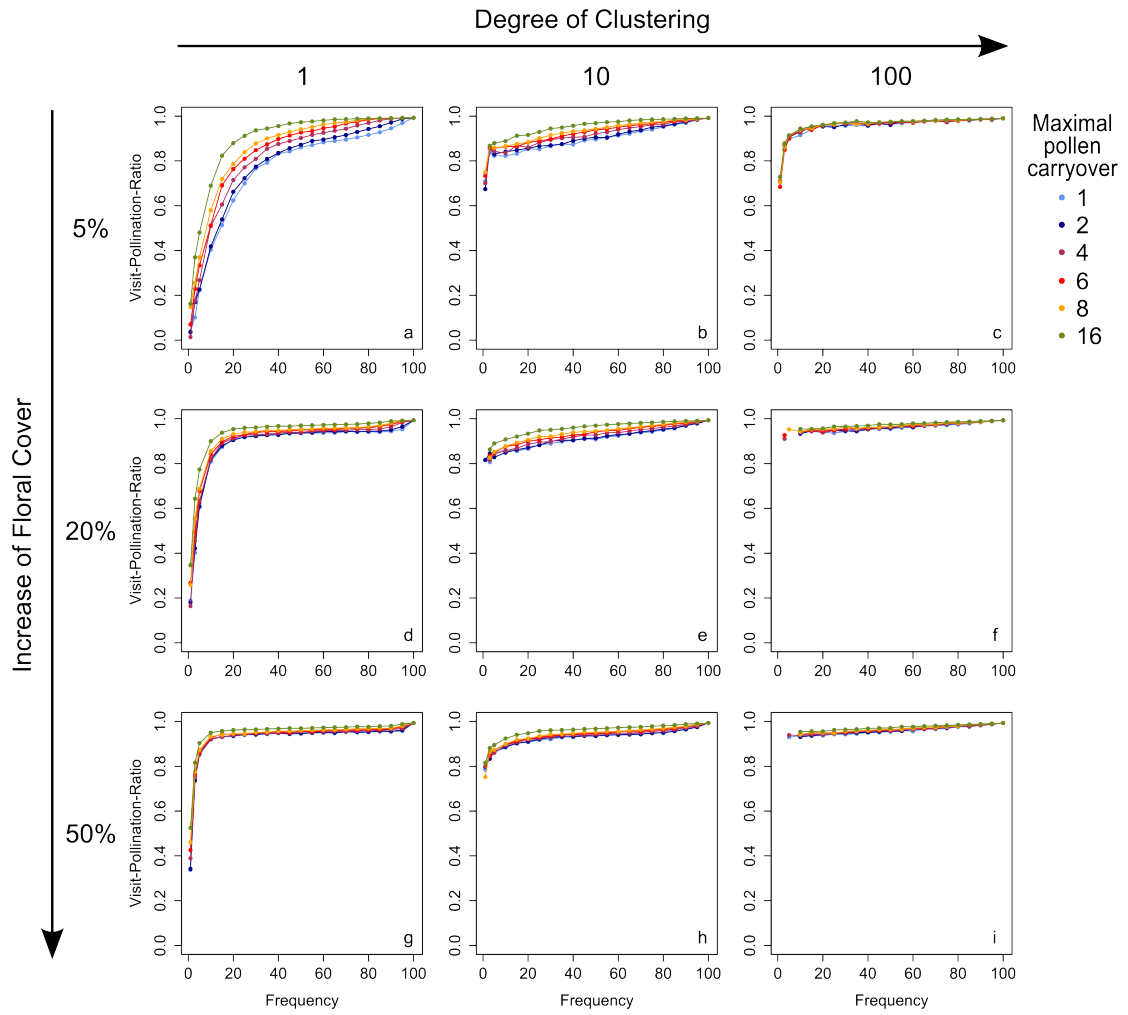


Figure 5: Frequency dependence of proportion of successful pollinator visits for different combinations of floral cover and cluster size. The pollen carryover value defines the maximum number of heterospecific visits within a successful pollination is possible. With a pollen-carryover rate of one, the pollen can only be carried to the next flower. Therefore, the ratio of successful pollinations per visit can be seen as indicator for flower constancy (Montgomery, 2009). A high pollen-carryover rate is only important for a low cover and no-cluster environment. With increasing cover and cluster, the ratio becomes steeper for low frequencies which stands for more qualitative visits.

Pollination Success

The degree of pollen carryover is defined as maximum number of heterospecific visits within a successful pollination can take place. In the model, I tested values from 1 (strong heterospecific pollen interference) to 16 (weak heterospecific pollen interference). Figure 5 gives the proportion of all visits where a successful pollination took place. The first 20% frequency are crucial for all parameter-value combination. A very steep increase up to 80% successful visits is followed by a moderate linear increase up to 100% for exclusive existence. The degree of pollen carryover only makes a difference for small cover and cluster values (Fig. 5a). The higher the cover and the bigger the clusters, the better is also the proportion of successful pollination, even for small frequencies, independent of the pollen-carryover rate (Fig. 5c,f,g-i).

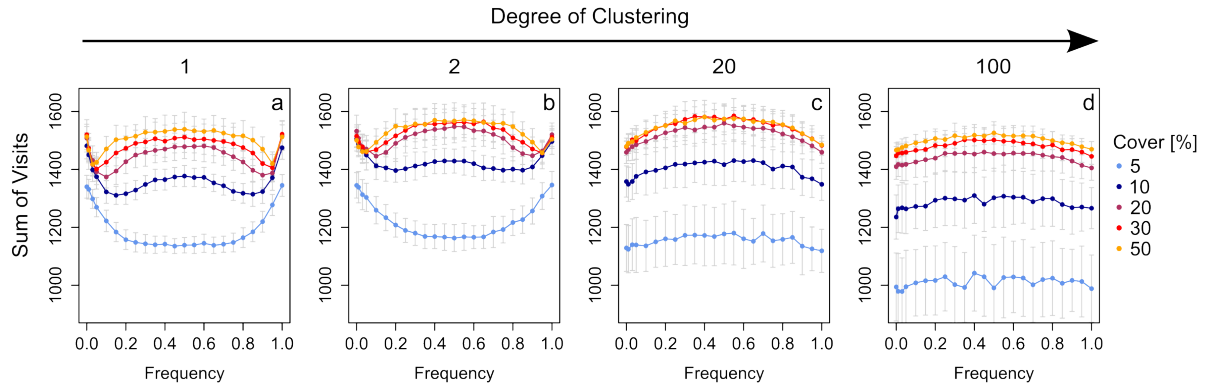


Figure 6: Summed visits to both species show a frequency dependence for low cluster values. Depending on the floral cover it is quadratic or a fourth-degree polynomial relationship. The maximum number of visits (maximal efficiency) is achieved for highly unequal or balanced frequencies of the two plant species, depending on floral cover and cluster size.

Global visitation

The sum of all visits to both plants together changes with the ratio of their abundance (Fig. 6). A strong cover-dependent pattern is visible for small cluster sizes. The total visits have an u-shaped relationship with frequency for 5% cover and a shape similar to a fourth-degree polynomial function for higher cover values. The visitation drops to a minimum at 90:10 ratio and peaks again for balanced frequencies. Cluster size reduces the frequency dependence.

Note that the mean number of total visits varies in addition to the shape for different values of cover and cluster size. Both parameters have a frequency independent influence on the visitation rate (Supplementary material, Fig. S4). Floral cover shows a saturated curve and the visits for degree of clustering have a hump-shaped relationship with a peak at an intermediate aggregation level of 5-10 flowers per cluster.

Sensitivity Analysis

Aim of the sensitivity analysis is to understand influence of behavioral rules on the outcome of the model. Therefore, pollinator density, reward regrowth, search time and vision were tested for a (unnaturally) broad range of values set in comparison to the empirically founded default values. Vision, search time and the number of bees on the meadow influence the sum of visits (Fig. S5). A larger range of vision leads to more visits, the search limit reduces the number of visits and more bees lead again to more visits per time unit. The reward function has a small negative influence on the total number of visits for a very high regrowth rate.

Furthermore, a very high replenishment rate (0.1J/sec, yellow line in Fig. S6) has a reversing effect on the frequency dependence: Rare species receive disproportionately few visits whereas common species benefit from a positive frequency dependence. The influence of frequency is less severe with increasing cluster size.

Every bee-agent can detect flowers in a 180° cone-shaped array of patches in front of them. The number of patches in that array is determined by the vision distance. A large range of vision increases the frequency dependence even in a heavily clustered model environment (Fig. S7). If the bee-agents are only able to see the direct neighbor, the frequency dependence is reversed to favor the common species for low cluster values.

If a bee-agent searches longer than a given search time limit unsuccessfully for a unvisited and preferred flower, the probability to switch preferences will increase by 10% with every additional step. The search limit was altered from 1 to 50 seconds in the sensitivity analysis. The results are similar to the effect of vision as they also change the probability to switch preferences. Higher search time limits lead to stronger negative frequency dependence benefiting the rare species. A search limit of 1 second reduces the dependency (Fig. S8).

Beside the expected increase of absolute visits, a change of pollinator density has no effect on the outcome of the model at any cover or cluster values (Fig. S9).

4 Discussion

Frequency dependence can influence the plants fitness and therefore have far reaching consequences for the development and maintenance of biodiversity. Aim of this thesis is to study the existence of frequency dependence in a natural plant community, explore the kind of relationship and identify the factors influencing frequency dependence with the help of an agent-based model.

I found evidence for frequency dependent pollination for rewarding flower species in grassland plant communities in the field data. The relationship is defined by a steep increase of visits within the first 20% frequency followed by a disproportional low gain of visits for every additional flower due to an increase of frequency. When the species becomes dominant the per-flower visitation rate increases again. The combination of negative and positive frequency dependence combined in a cubic curve is generally supported by the agent-based model. Furthermore, the model reveals floral cover and cluster size as important influencing factors for frequency dependence.

Previous research found positive frequency dependence for lab experiments on rewarding flowers and inconsistency in the few field experiments focusing on color morphs (Smithson, 2001). However, the field data shows a cubic pattern of frequency dependency for at least four different rewarding flower species and the results from the foraging simulation support the general shape of the per-flower visitation ratio. Where does the discrepancy of lab and field data comes from?

The sensitivity analysis of the agent-based model can give an explanation: If the reward function is increased to a refill within 10 time steps, the relationship is reversed to a positive frequency dependence and the rare species receives disproportionately few visits (Fig. S6). The curve is consistent with findings of Smithson and MacNair (1997a) and Smithson and Macnair (1996). In their study design, artificial flowers were refilled after each foraging bout. Therefore, every bumble bee foraged on a set of full and equally rewarding flowers which is comparable to a high regrowth function in the agent-based model.

We know that pollinators more likely abandon flower constancy if they experience sequentially bad reward (Chittka et al., 1997; Goulson, 1994). If the reward is always high, pollinators have less incentive to go on exploratory visits to the rare species as the abundant type is easy to find and sufficient rewarding. Hence it can be assumed that negative frequency dependent selection does not exclusively apply for non-rewarding species but also for flowering communities with varying or insufficient reward. Strong positive frequency dependence in pollination might be only possible for highly rewarding or artificial systems.

Floral cover and cluster size are influencing factors

The model reveals two main influences for frequency dependence: The higher the floral cover, the stronger the frequency dependence and the bigger the clusters, the weaker the frequency dependence (Fig. 4e-h). Floral density is known to influence visitation rates, usually positive and with a saturating function (eg. Rathcke 1983; Essenberg 2012; Bernhardt et al. 2008; Kunin 1997). Those findings are consistent with the Hollings type II functional response found for different cover values (Supplementary material, Fig. S4a). If the cover is increasing, the absolute number of flowers rises also for the rare species. That makes it more likely for a bee-agent to find a flower before changing preference towards the common species due to long search times even if foraging on the later would be more efficient. Therefore, high cover causes the same effect as expanded vision distance or maximum search limit (cf. Fig. S7 and Fig. S8): The main reason of abandoning flower constancy becomes multiple visit of flowers with low reward. Consequence are explanatory visits to the rare species which can have a great impact on the per-flower visitation rate. Every visit to a rare species weights high in the per-flower visitation rate because the sum of visits is divided through the number of flowers.

The model shows that spatial aggregation of flowers can lead to a more efficient foraging (more visits per time unit), less frequency dependence and a higher quality of visits due to compatible pollen deposits. If flowers are randomly distributed over the whole meadow, many short search and flight times apply. An intermediate cluster level is easy to exploit by a pollinator whereas the flight and search times can be very long in between few big clusters, especially for low floral densities.

It was already suggested by Epperson and Clegg (1987) that spatial agglomeration of flowers decreases frequency dependence. In the agent-based model, a similar effect compared to low cover takes place: If flowers are aggregated at few places, they affect the pollinators perception of frequency and are more difficult to find.

Long search times will weaken the bee-agents flower preference and lead to foraging on the next available cluster independent of its species.

Requirements for successful pollination

High visitation rate is gained at low frequency with high cover and low cluster size. However, those visits might not be the best quality if the pollination per visit ratio is comparatively low (Fig. 5a,d). The ratio can be seen as index for flower constancy: If the majority of visits lead even for a small pollen carryover value to successful pollination the bee-agents forage very flower constant (Montgomery, 2009). If the cover is high, bee-agents will keep their constancy also for rare species because they are abundant enough. If the aggregation of flowers is high, bee-agents exploit this cluster before leaving for the next. Every visit within a cluster of flowers of the same species is counted as successful pollination and can lead to a high visit quality even if the cover is low (cf. Jakobsson et al. 2009). Therefore, rare species should occur in clusters of flowers if the cover is low to get a maximum of pollination per visit. If the cover is high the spatial distribution plays a minor role for the visit quality.

Sum of visits to the flower community also show frequency dependence

Additionally to individual frequency dependence, I analyzed the impact of species partitioning on frequency dependent visitation in the system as whole.

If the cover is very low, a maximum in total visits can be received if one species is dominant. Co-flowering will lead to longer search times and less overall visits (u-shape for 5% cover in Fig. 6a). For higher cover, the frequency dependence shows a function similar to a fourth-degree polynomial. If one species is rare at 5-20% frequency, pollinators exhibit exploratory visits to the rare species and spend inefficient time searching. Hence, the total visitation number drops to a minimum. If species are evenly distributed the pollinators forage on both species in equal amounts. This is the most efficient status for the overall ecosystem, especially for high cover or cluster size.

Spatial aggregation weakens the frequency effect but will also reduce the total visits. If flowers are even and random distributed, the bee-agent has many small search times intermittent by collecting reward on a single flower and continue foraging. Rare flowers can be found comparatively easy if they are spread over the whole meadow and flower constancy will be kept even if it is highly inefficient. If the clusters of flowers are bigger, bee-agents will not find rare flowers that easily because they might occur only in a single cluster on the meadow. The bee-agent switches to the common flower, the minimum at very uneven distribution disappears and the relationship becomes slightly hump-shaped (Fig. 6b,c).

A maximum of overall visits favoring both the pollinators and the co-flowering plants can be achieved with balanced abundance in high cover and very uneven species distribution for low floral cover environments.

Limitations of the study design and research suggestions

Even though modeling can be an excellent tool to understand and interpret ecological data, some questions evolve comparing the data collected in the Jena Experiment and the foraging model. Floral cover is an important factor in the outcome of the model. It influences not only the absolute number of visits but also the intensity of frequency dependence. But it was removed in the model selection as it was no factor of explanatory power to the per-flower visitation data. Reason could lie in the sampling design. Data was only observed from plots with an intermediate cover, no extremes were taken into account. In total, there were only five values for cover in the final analysis. Also all cover values are estimations, no exact measurements. Also, pollinators are influenced by many factors in the field, not all of them measured in this study or possible to take into account at all. Other floral traits like scent, the pollinators detection of colors and differences in pollinator types are just some factors which might have an impact on the foraging behavior and consequently also on frequency dependence. (Smithson, 2001).

Validation of further results of the agent-based model can be made via a supplementary study with varying frequency, cover and cluster size of two co-flowering species. Practical is a simplified study design with less influencing variables either under natural conditions where manipulation is possible (eg. Eckhart et al. 2006; Essenberg 2012) or with potted plants (Epperson and Clegg, 1987). Also results of the frequency dependent sum of visits could be tested by manipulated field experiments. Natural conditions data are not suitable

for this purpose because every plot contains more than two co-flowering species with unequal attractiveness. The data collected in Jena shows drastic differences in attractiveness of the focal species and frequency dependence was found to be subject to each species. Therefore I suggest continuous research on a variety of species, both rewarding and unrewarding with measurements of reward to check if my findings are universally valid.

5 Conclusions

In conclusion, this study shows for the first time that frequency dependent selection exists in natural flowering communities for rewarding species. Also, a combination of methods is exceptionally helpful to understand influencing factors. Both, the output of the agent-based foraging model and the results of the field data show a cubic influence of frequency on the per-flower visitation rate. More pollinator visits can lead to more seeds, give an advantage in the lottery competition in reproduction and therefore influence the fitness of a species. The sensitivity analysis can fill some knowledge gaps in previous research: Positive frequency dependence proved multiple times in lab experiments is likely due to very high rewards and low cover values. Hence, negative frequency dependence is not exclusive to non-rewarding morphs but takes effect also for rewarding species if the reward is not exceptionally high or the cover is very low.

Positive and negative frequency dependence may not be object to certain species. The results suggest that it is more likely that patterns change across space and time, especially because the model revealed floral cover as increasing and spatial aggregation of flowers reducing factor. If frequency dependence is in fact found for a variety of rewarding flowers not only floral polymorphisms, I agree with Eckhart et al. (2006) that it might be more important in the evolution and conservation of diversity than previously recognized.

Further research is necessary to validate the role of floral cover and cluster for frequency dependence. A controlled field experiment including measurements of floral reward and pollination success could be a suitable approach. Based on the findings, I would also recommend the connection of modeling, field and lab work. Most research is only done in one of those three approaches with a lack of cross-validation. A great deal of knowledge could be gained by establishing interdisciplinary working groups of field ecologists and environmental modeling experts.

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Supplementary Material

Table S1: List of the focal species observed in the natural condition experiment within the Jena Experiment. Species had to flower in at least five plots with different frequency values to be considered as focal species.

Short	Name	German Name	Order	Family	Color
Ger	<i>Geranium pratense</i>	Wiesen-Storchschnabel	Geraniales	Geraniaceae	Purple
Lat	<i>Lathyrus pratensis</i>	Wiesen-Platterbse	Fabales	Fabaceae	Yellow
Lot	<i>Lotus corniculatus</i>	Gewöhnlicher Hornklee	Fabales	Fabaceae	Yellow
Ono	<i>Onobrychis viciifolia</i>	Saat-Esparsette	Fabales	Fabaceae	Pink+White
TP	<i>Trifolium pratense</i>	Wiesen-Klee	Fabales	Fabaceae	Purple

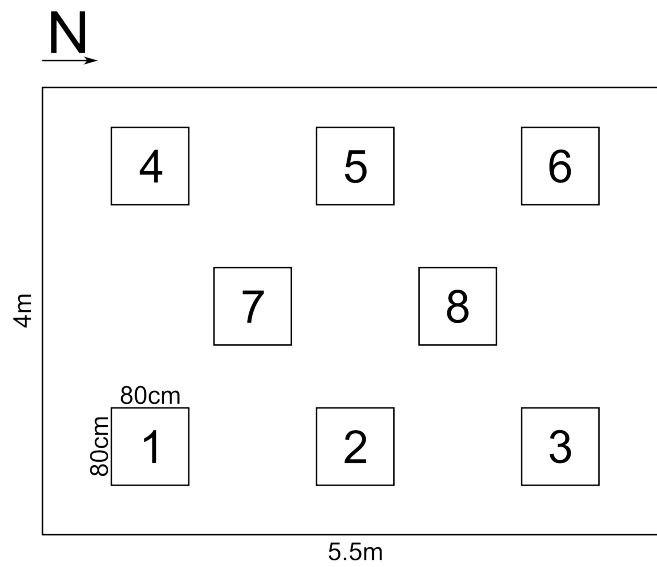


Figure S1: The distribution of patches within the old invasion plots.

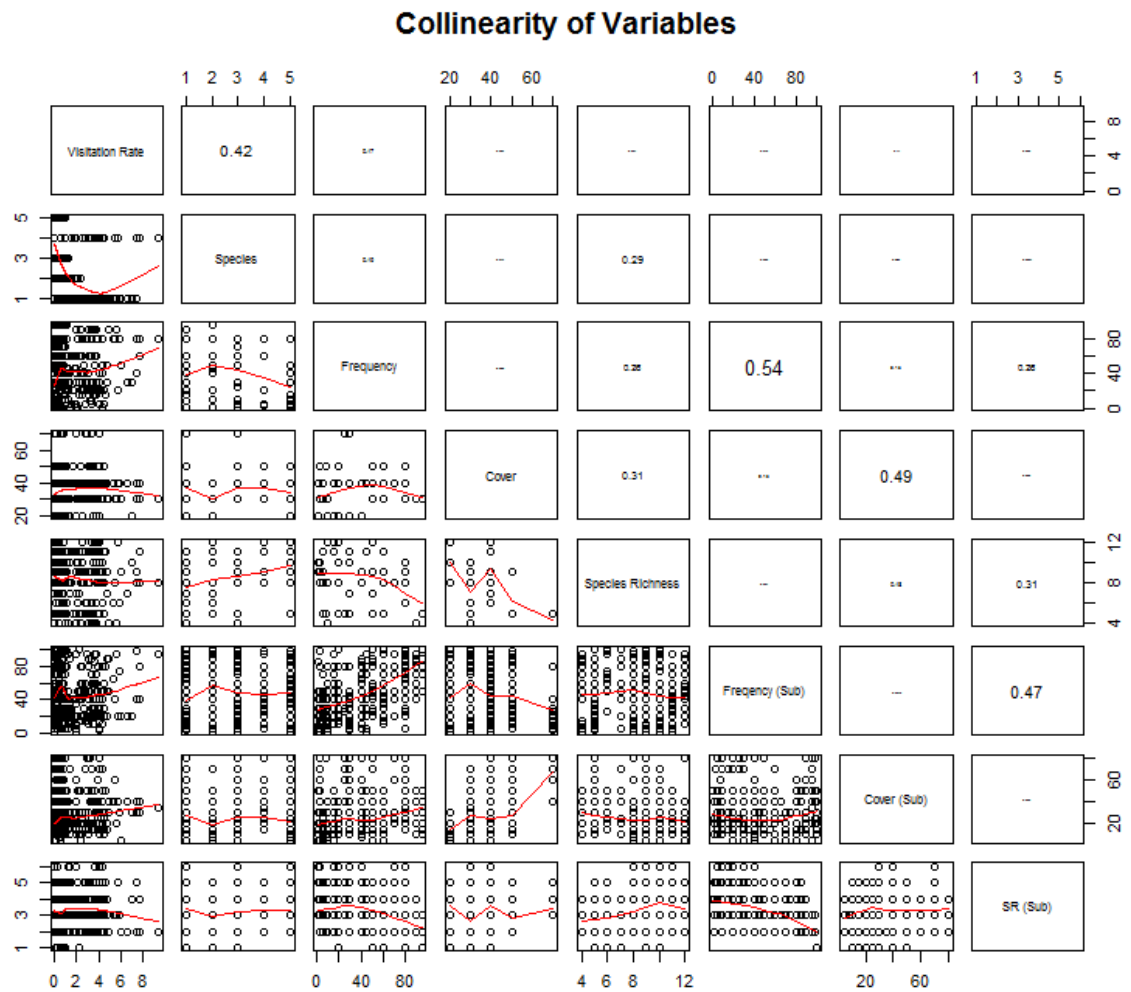


Figure S2: Pairwise correlation of per-flower visitation rate (response variable), species, frequency, floral cover and species richness on plot and patch level. The upper panels contain Pearson correlation coefficients with its size proportional to its value. Parameters correlate on the plot and subplot level but show no strong correlation not among each other.

Table S2: Variance inflation factors (VIF) for the full set of variables. Values are calculated by the "corvif"-function from R-package AED. All values are well below three indicating no collinearity (see Zuur et al. 2007).

Variable	GVIF
Visitation Rate	1.26
Species	1.36
Frequency	1.63
Floral Cover	1.46
Species Richness	1.45
Frequency (Patch)	1.84
Floral Cover (Patch)	1.37
Species Richness (Patch)	1.48

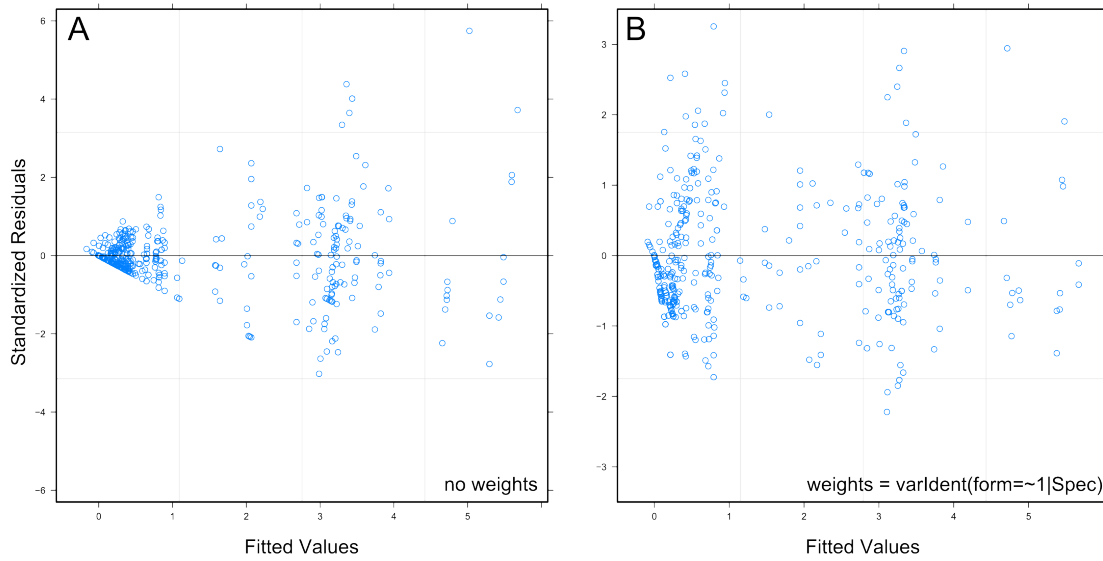


Figure S3: Standardized residuals plotted against fitted values for the final mixed effect model with and without applied weighting. A) Without weighting, the residuals show strong pattern of heteroscedasticity. B) The weighting allows different variance per species. The final model is significantly better with weighting ($L=393.32$, $df= 4$, $P < 0.0001$)

Table S3: Extended output from the linear mixed effect model. Floral cover, species richness and its interactions were removed in the model selection.

Expanatory Variables	Estimate	\pm SE	<i>P</i>
Intercept (Ger)	1.41	0.49	0.0048
Lat	-1.58	0.58	0.0069
Lot	-1.38	0.51	0.0075
Ono	-1.31	1.06	0.2182
TP	-1.39	0.5	0.0060
Frequency	0.11	0.05	0.0147
Frequency ²	-0.002	< 0.01	0.0699
Frequency ³	< 0.01	< 0.01	0.1174
Frequency x Lat	-0.09	0.05	0.0925
Frequency x Lot	-0.09	0.05	0.0687
Frequency x Ono	0.32	0.14	0.0183
Frequency x TP	-0.1	0.05	0.0425
Frequency ² x Lat	< 0.01	< 0.01	0.1013
Frequency ² x Lot	< 0.01	< 0.01	0.2053
Frequency ² x Ono	-0.01	< 0.01	0.0113
Frequency ² x TP	< 0.01	< 0.01	0.1479
Frequency ³ x Lat	> -0.01	< 0.01	0.0966
Frequency ³ x Lot	> -0.01	< 0.01	0.2996
Frequency ³ x Ono	< 0.01	< 0.01	0.0086
Frequency ³ x TP	> -0.01	< 0.01	0.2283

Table S4: The full set of parameters and default values used in the model.

Parameter	Description	NetLogo-Type	Type	Value	Reference
SETUP PARAMETERS:					
area	"world" in NetLogo, defined by a grid of cells called patches		integer	100x100	
patch-size	Size of one grid-cell in NetLogo. Can be either a flower or grass		float	0.1m ²	
tick	One time-unit in NetLogo		integer	1s	
flower-cover	Proportion of grid cells containing a flower	global	integer	5, 10, 20, 30, 50	
frequency	Proportion of flowers which are species A ($Frequency = 100 - Frequency_A$)	global	integer	0-100%	
cluster-number	Average number of flowers per cluster	global	integer	1, 2, 5, 10, 20, 50, 75, 100	
number-bees	Initial number of pollinators in the model	global	integer	10	0.0004 - 1 bee/m ² (Essenberg, 2012)
BEHAVIOURAL PARAMETERS:					
search-speed	Distance a pollinator can move per time step	bees-own	integer	0.1m /sec	Kunin 1991 in Kunin and Iwasa 1996 0.09-0.17 (Essenberg, 2012)
stdev-angle	Standard deviation for the normal distribution used in the CRW	global	integer	30	Waddington 1980
flightsteps-until-change	Seconds of unsuccessful search before the preference changes	bees-own	integer	5s (= 5 ticks)	Chittka et al. 1997; Kunin 1993
length-memory	How many flowers can a bee remember to avoid double-visiting	bees-own	integer	4	Goulson 2000, see Goulson 1999 for review
view	Value for the radius of grid-cells a pollinator can see (cone-view of 180°)	bees-own	integer	0.7m (= 6 grid-cells)	Dyer et al. 2008; Wertlen et al. 2008 Ne'eman and Kevan 2001
array	Array of all suitable flowers (referred, non-visited) in sight of the pollinator	bees-own	Array		
reward-function	How much reward is replenished per second	flowers-own	float	0.00004 J/s	
handling-time	The time a pollinator needs for exploiting the floral reward	bees-own	integer	reward * 4s + 0.5s (+ 3s)	Roubik 1992 in Kunin and Iwasa 1996
reward	Reward in Joule the flower has to offer. Exploited with each visit, replenished over time	flowers-own	float	reward(max) = 1J	Kunin 1991 in Kunin and Iwasa 1996
pollen carry-over rate	Number of heterospecific visits within a successful pollination is possible	flowers-own	integer	1, 2, 4, 6, 8, 16	Benadi et al. 2012
flower-memory	A list of flower-locations	bees-own	string	4	see Goulson 1999 for review
reward-memory	A list of the last gained rewards	bees-own	string	4	
change-prob	Probability to change the preferred flower type. Increases with low reward and long search times	bees-own	float		
choice	Current flower choice for the pollinator (for constancy)	bees-own	boolean		

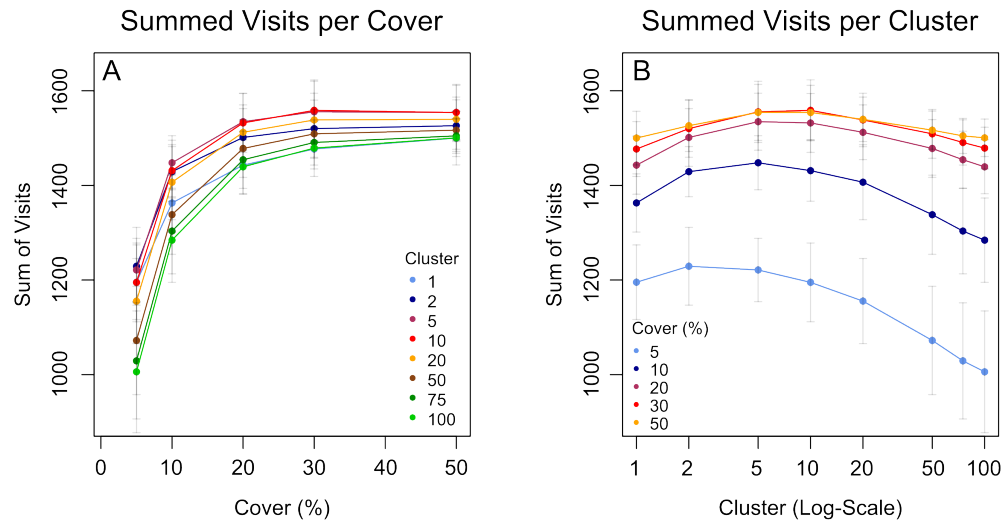


Figure S4: Frequency independent influence of floral cover and cluster size on the sum of all visits to both species together. A) Cover strongly influences the number of visits as it reduces the flight and search time and shows a saturated relationship for all cluster values. This matches the Holling's type II functional response. B) The degree of clustering influences the sum of visits in a hump-shaped function. The maximum lays between 5 and 10 flowers per cluster (depending on the cover). A small aggregation of flowers reduces search times but keeps the next patch within visible distance. The bigger the cluster, the more difficult for the bee-agent to find the next one.

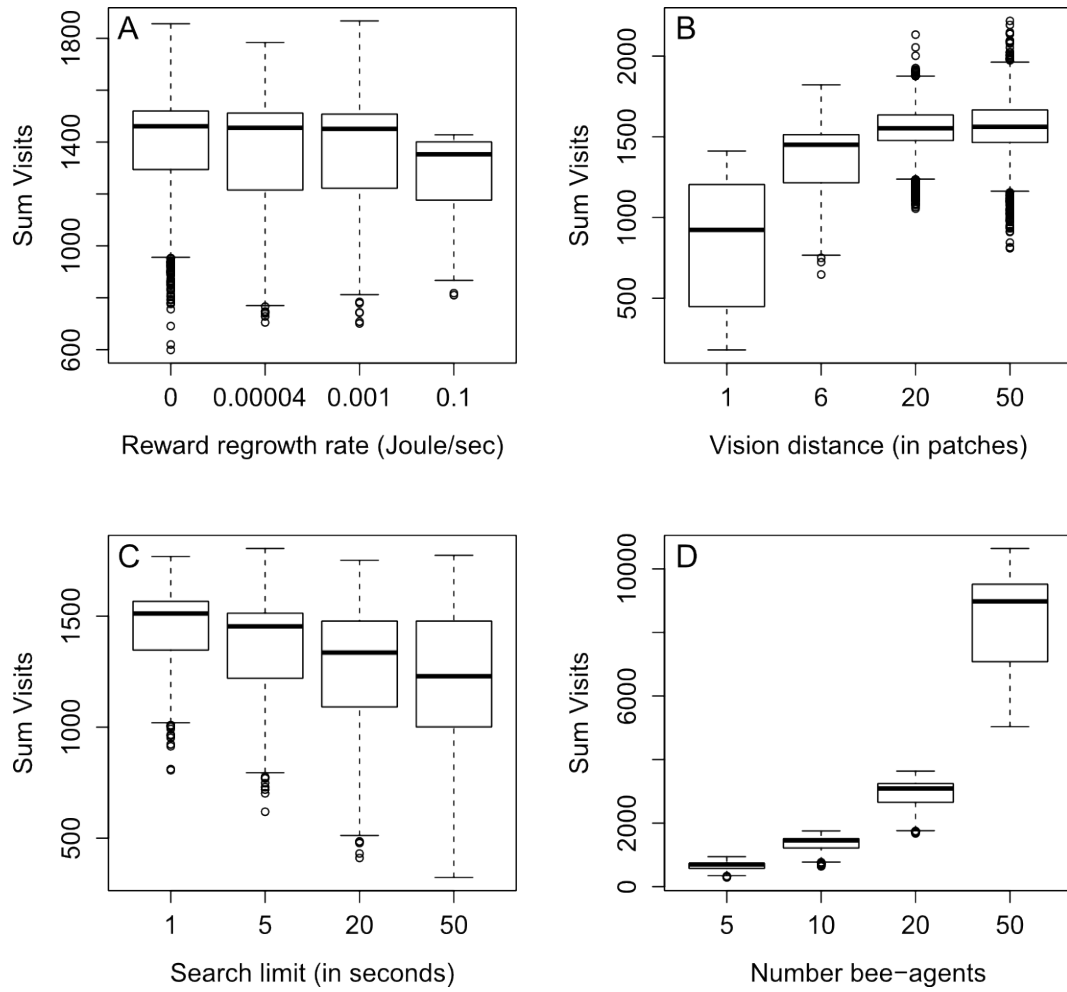


Figure S5: The influence of reward replenishment, vision, search limit and number of bee-agents on the sum of visits within a 1000 time-step simulation run. A) An unnatural high reward replenishment rate (if the flowers are refilled within 10 time steps) has a small negative influence on the visits. B) Bee-agents with a far field of view can detect flowers faster, move in a direct way towards them and be therefore more efficient. However, the curve is saturated at a view of 20 patches. C) An increase in search time limit decreases the sum of visits and spread the variance. Bees-agents will keep searching for rare flowers instead of switching to the common species. D) As assumed, more bees lead to more visits.

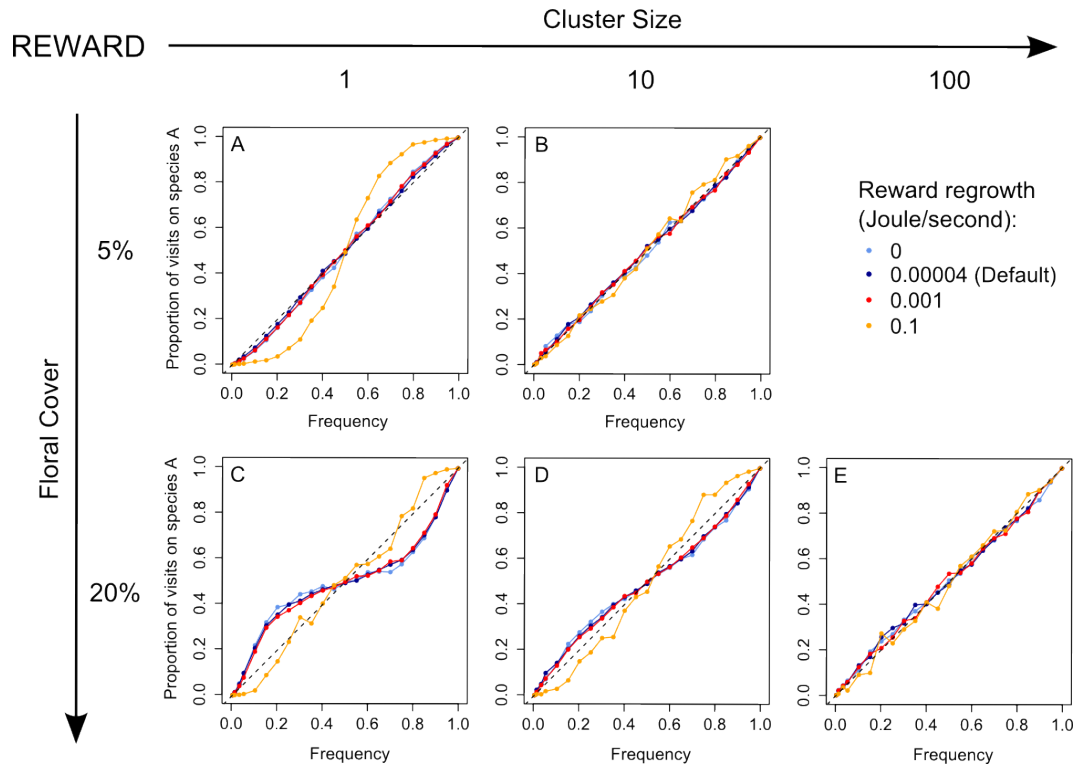


Figure S6: Outcome of the model if the reward replenishment function is changed to 0, 0.0004, 0.001 and 0.1 Joules per time step. Only the unnatural high reward function (complete regrowth after 10 seconds) has an influence on the frequency dependence: The bee-agents have no more reason to change preference due to bad reward. This favors the more common species as shown in the opposite curving for no-cluster environments. A lower replenishment rate has no effect.

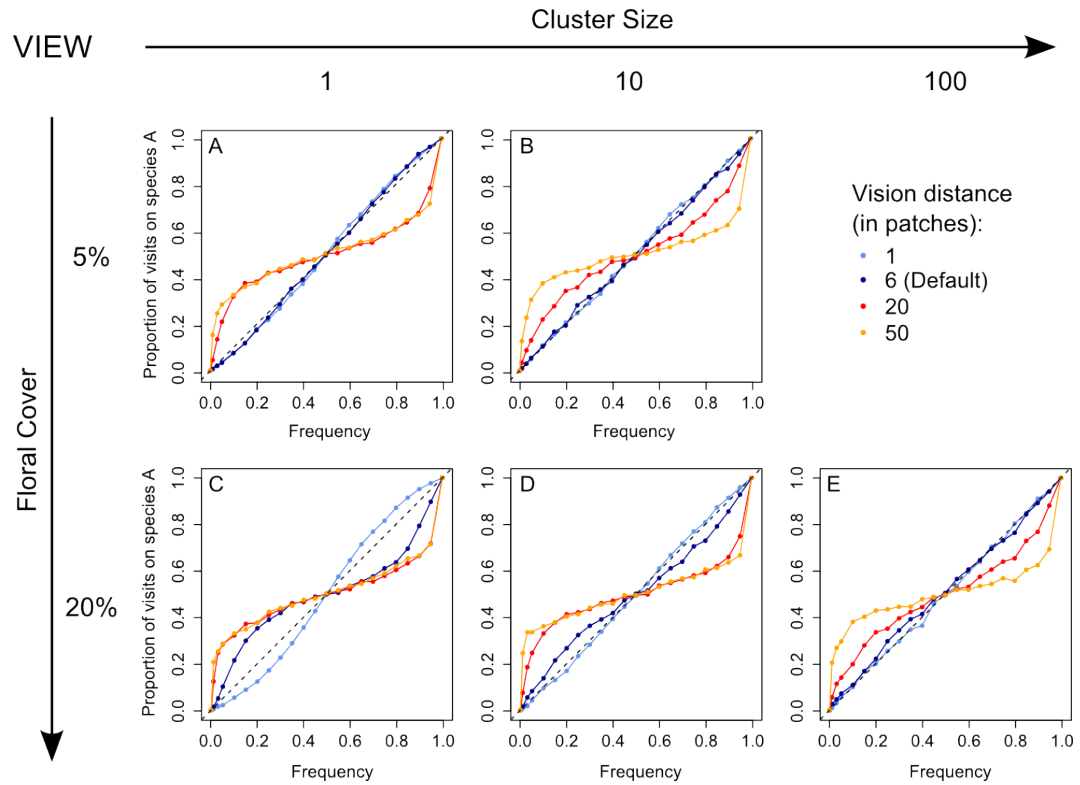


Figure S7: Effect of increased or reduced vision for the bee-agent. The vision influences the behavior of the bee-agent. If it sees far, it can move on direct way towards the next preferred flower and saves searching time. But it also flies longer distances instead of changing to the common species. A large vision therefore increases the frequency dependence and a very low vision shifts the advantage towards the more abundant species.

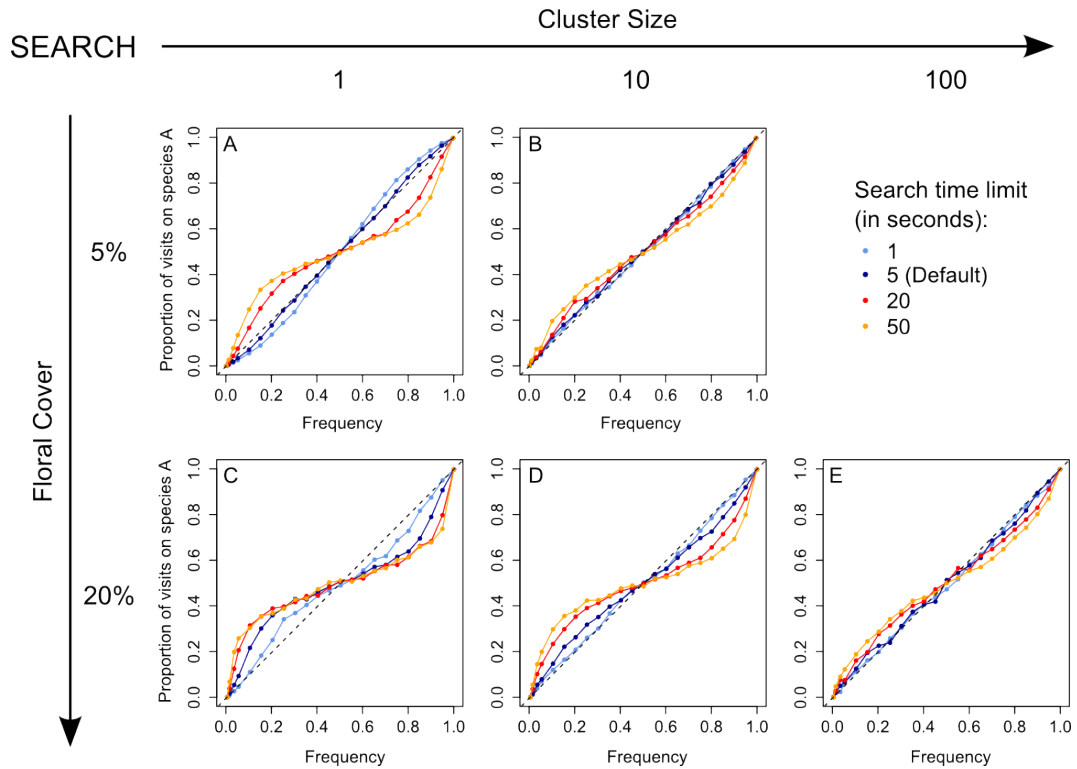


Figure S8: Sensitivity analysis for search limits of 1, 5, 20 and 50 seconds. The search limit is the number of seconds within a bee-agent searches for a unvisited and preferred flower, moving around the meadow by a correlated random walk. After the search limit is reached, the probability to change its flower preference increases with every additional second of unsuccessful search by 10%. The search limit has a similar effect on the outcome of the model as the vision because it also influences the change probability. With a higher search time, the bee-agent continues searing instead of switching to the more abundant flower, the frequency dependence is increased. A higher cluster value weakens the effect.

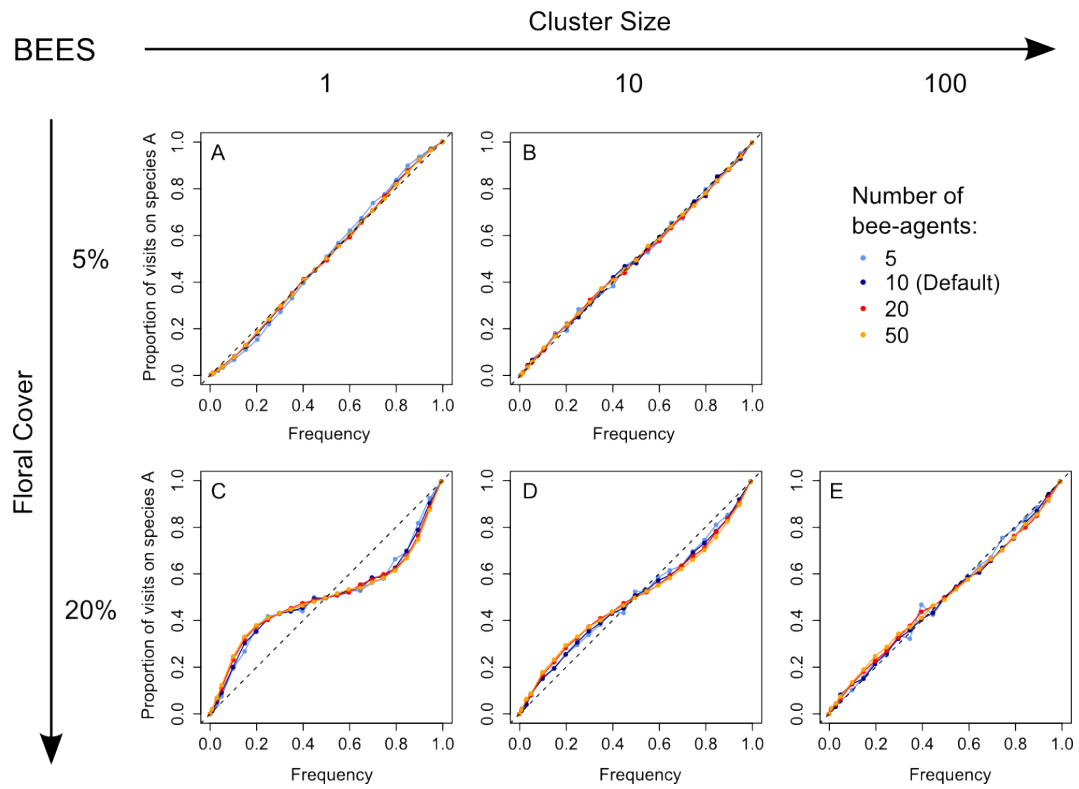


Figure S9: Results of the model for 5, 10, 20 and 50 bee-agents on the meadow. The proportion of visits does not change, only the absolute numbers. Therefore has the pollinator density no influence on the frequency dependence.

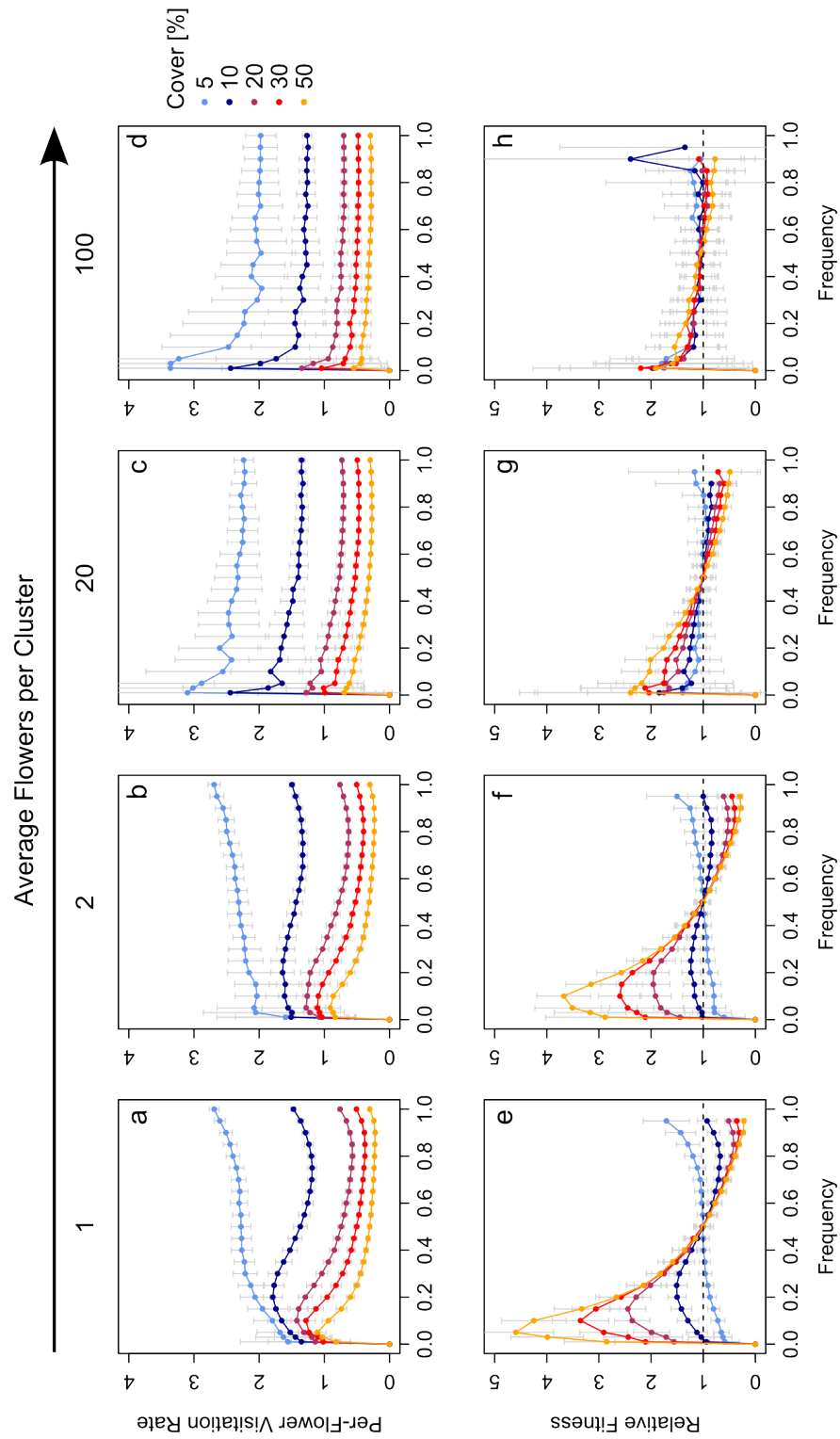


Figure S10: Enlarged version of Figure 4. The per-flower visitation rate shows a frequency dependence with a cubic relationship. The same data is plotted relative to per-flower visitation of the other species to visualize the relative fitness and intensity of frequency dependence (e-h).

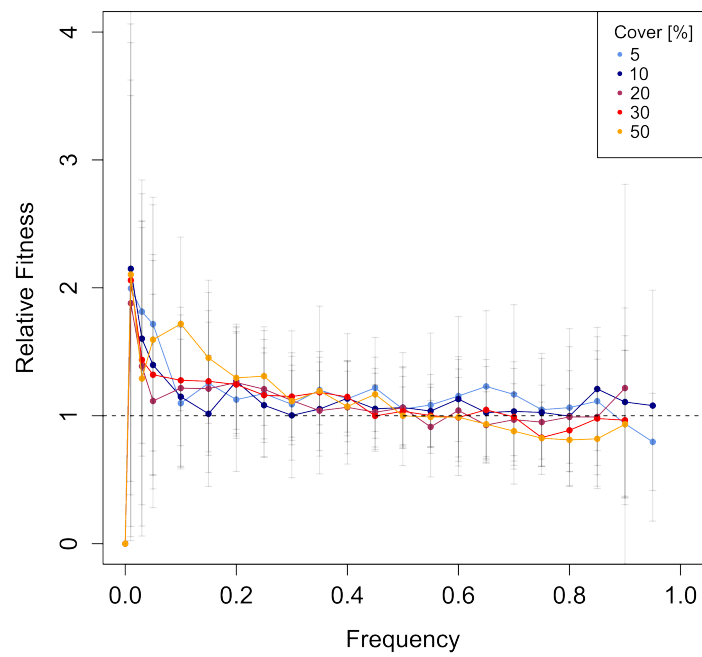


Figure S11: Results of the model for an average of 100 flowers per cluster. The per-flower visitation of species A was divided through the per-flower visitation of species B to observe the relative fitness. Due to a statistical outlier in the main analysis (Fig. 4h), the model was run again with 50 runs per parameter combination. Points are the mean of all runs with grey error bars.

Code

Jena Analysis

```
1 #packages
2
3 install.packages("nlme")
4 install.packages("MASS")
5 install.packages("mgcv")
6 install.packages("lattice")
7 install.packages("ggplot2")
8 install.packages("multcomp")
9 install.packages("MuMIn")
10
11 library(MASS)
12 library(mgcv)
13 library(nlme)
14 library(lattice)
15 library(ggplot2)
16 library(multcomp)
17 library(MuMIn)
18
19 #data and adjustments
20
21 jena <- read.csv2("C:/Users/hczioska/Documents/GitHub/Data/jena/data1.csv", header=T, sep=
22 ";")
23 names(jena)
24
25 jena$PatchID <- as.factor(jena$PatchID)
26 jena$Instead <- as.factor(jena$Instead)
27 jena$PatchID <- as.factor(jena$PatchID)
28 jena$Date <- as.POSIXct(paste(jena$Year, jena$Month, jena$Day, sep=" "),
29 format="%Y %an %d") # Datum in R-Format
30
31 #possible response-variables:
32 jena$Sum_all_visits <- jena$Bees_spec + jena$Bees_other +
33 jena$Bombus_spec + jena$Bombus_other + jena$Hoverfly_spec +
34 jena$Hoverfly_other + jena$Rest_spec + jena$Rest_other
35
36 jena$Sum_spec_visits <- jena$Bees_spec + jena$Bombus_spec +
37 jena$Hoverfly_spec + jena$Rest_spec
38
39 jena$Spec_visit_share <- jena$Sum_spec_visits / jena$Sum_all_visits
40
41 jena$VR_spec <- jena$Sum_spec_visits / jena$Number_Flowers
42
43 jena$VR_spec_apis <- jena$Bees_spec / jena$Number_Flowers
44 jena$freqshare <- jena$Freq_Plot / 100
45 str(jena)
46
47 write.csv(jena, "C:/Users/hczioska/Documents/GitHub/Data/jena/jena.csv", row.names=F)
48
49 #some basics on the data
50
51 length(unique(jena$Date)) #15 Sampling-Days
52 length(unique(jena$PlotID)) #23 different Plots
53
54 max(jena$SR_Plot) #12
55 min(jena$SR_Plot) #4
56 sd(jena$SR_Plot) #2.4
57 mean(jena$SR_Plot)
58
59 max(jena$SR_Patch) #8
60 min(jena$SR_Patch) #1
61 sd(jena$SR_Patch) #1.16
62 mean(jena$SR_Patch)
63
64 length(jena[which(jena$VR_spec == 0),])
65
66 max(jena.lat$VR_spec)
```

```

66 min(jena.lat$VR_spec)
67 sd(jena.lat$VR_spec)
68 mean(jena.lat$VR_spec)
69 nrow(jena.lat)
70
71 pairwise.t.test(jena$VR_spec, jena$Spec)
72
73 max(jena$Sum_spec_visits)
74 min(jena$Sum_spec_visits)
75 sd(jena$Sum_spec_visits)
76 mean(jena$Sum_spec_visits)
77
78 #data-subsets
79
80 jena.ono <- jena[which(jena$Spec == "Ono"),]
81 jena.lat <- jena[which(jena$Spec == "Lat"),]
82 jena.lot <- jena[which(jena$Spec == "Lot"),]
83 jena.ger <- jena[which(jena$Spec == "Ger"),]
84 jena.tp <- jena[which(jena$Spec == "TP"),]
85
86 jena.ono <- jena.ono[order(jena.ono$Freq_Plot),]
87 jena.lat <- jena.lat[order(jena.lat$Freq_Plot),]
88 jena.ger <- jena.ger[order(jena.ger$Freq_Plot),]
89 jena.tp <- jena.tp[order(jena.tp$Freq_Plot),]
90 jena.lot <- jena.lot[order(jena.lot$Freq_Plot),]
91
92 #####
93 ###ANALYSIS#####
94 #####
95 # following Zuur 2009
96
97 # 1. check for collinearity
98
99 z <- cbind(jena$VR_spec, jena$Spec, jena$Freq_Plot,
100           jena$Cover_Plot, jena$SR_Plot, jena$Freq_Patch,
101           jena$Cover_Patch, jena$SR_Patch)
102
103 colnames(z) <- c("Visitation Rate", "Species", "Frequency",
104                 "Cover", "Species Richness", "Frequency (Sub)",
105                 "Cover (Sub)", "SR (Sub)")
106
107 z <- z[complete.cases(z),]
108
109 panel.cor <- function(x, y, digits = 2, prefix = "", cex.cor, ...)
110 {
111   usr <- par("usr"); on.exit(par(usr))
112   par(usr = c(0, 1, 0, 1))
113   r <- abs(cor(x, y))
114   txt <- format(c(r, 0.123456789), digits = digits)[1]
115   txt <- paste0(prefix, txt)
116   if(missing(cex.cor)) cex.cor <- 0.9/strwidth(txt)
117   text(0.5, 0.5, txt, cex = cex.cor * r)
118 }
119
120 pairs(z, lower.panel = panel.smooth,
121       upper.panel = panel.cor, main="Collinearity of Variables")
122
123 #check VIF:
124 colnames(z) <- c("Visitation_Rate", "Species", "Frequency",
125                 "Cover", "Species_Richness", "Frequency_Sub",
126                 "Cover_Sub", "SR_Sub")
127
128 source("C:/Users/hczioska/Documents/HighstatLibV6.R") #corvif aufrufen
129 corvif(z)
130
131 #"All VIF values are below 3 (see Chapter 26 in Zuur et al. (2007)), indicating there is no
132   collinearity in these variables"
133
134 # 2. The beyond optimal model

```

```

135 fALL <- formula(VR_spec ~
136                 Freq_Plot+
137                 I(Freq_Plot^2)+
138                 I(Freq_Plot^3)+
139                 Spec+
140                 Cover_Plot+
141                 SR_Plot +
142                 Freq_Plot:Cover_Plot+
143                 Freq_Plot:SR_Plot+
144                 Freq_Plot:Spec+
145                 I(Freq_Plot^2):Spec+
146                 I(Freq_Plot^3):Spec+
147                 I(Freq_Plot^2):Cover_Plot)
148
149 #I am using a mixed model because I have 8 observation per Plot.The data is therefore not
      independent but nested.
150
151 lmeALL <- lme(fALL,random=~1|PlotID/PatchID, data=jena)
152
153 # 3. Model Validation Nr. 1
154
155 plot(lmeALL)
156 #Problem: Strong Heterogeneity / Heteroscedasticity!!
157 #violates the homogeneity of variance assumption
158 #MFollowing Zuur 2009 chapter 4 (p.72 ff & Appendix p. 535) —> Adjustment of weights
159
160 # 4a. Applying different weights
161
162 M.original <- gls(fALL, data=jena)
163
164 fixed <- varFixed(~Freq_Plot)
165 M1.fixed <- gls(fALL, data=jena, weights=fixed)
166 #Not possible for Spec because it is a factor
167
168 varFreq <- varIdent(form=~1|Freq_Plot)
169 M1.varFreq <- gls(fALL, data=jena, weights=varFreq)
170
171 varSpec <- varIdent(form=~1|Spec)
172 M1.varSpec <- gls(fALL, data=jena, weights=varSpec)
173 #each species is allowed to have a different variance
174
175 varCov <- varIdent(form=~1|Cover_Plot)
176 M1.varCov <- gls(fALL, data=jena, weights=varCov)
177 #each species is allowed to have a different variance
178
179 varP <-varPower(form=~Freq_Plot|Spec)
180 M1.varP <- gls(fALL, data=jena, weights=varP)
181
182 varPf <-varPower(form=~Freq_Plot)
183 M1.varPf <- gls(fALL, data=jena, weights=varPf)
184
185 varE <- varExp(form=~Freq_Plot)
186 M1.varE <- gls(fALL, data=jena, weights=varE)
187
188 varCP <- varConstPower(form=~Freq_Plot)
189 M1.varCP <- gls(fALL, data=jena, weights=varCP)
190
191 varCPs <- varConstPower(form=~Freq_Plot|Spec)
192 M1.varCPs <- gls(fALL, data=jena, weights=varCPs)
193 #Constant plus power of the variance covariate
194
195 varCom <- varComb(varIdent(form=~1|Spec),varExp(form=~Freq_Plot))
196 M1.varCom <- gls(fALL, data=jena, weights=varCom)
197
198 varCom2 <- varComb(varFixed(~Freq_Plot), varIdent(form=~1|Spec))
199 M1.varCom2 <- gls(fALL, data=jena, weights=varCom2)
200
201 # 4b. Results weights
202
203 AIC(M.original,M1.fixed, M1.varFreq, M1.varSpec, M1.varCov,

```

```

204 M1.varP, M1.varPf, M1.varE, M1.varCP, M1.varCPs,
205 M1.varCom, M1.varCom2)
206
207 #best is varCPs, second varSpec (varIdent)
208 #Ecologically it makes sense to choose varIdent! Spec is a nominal variable with very
    different values for each species. VarIdent allows different residual variation for
    the visitation rate per focal species
209
210 #Include it in the mixed model:
211 M1 <- lme(fALL, random=~1|PlotID/PatchID,
212          data=jena, weights = varSpec)
213 M2 <- lme(fALL, random=~1|PlotID/PatchID,
214          data=jena, weights=varCPs) #does not work, too few data
215
216 anova(lmeALL,M1)
217
218 plot(M1)
219 plot(lmeALL)
220 #great difference, weighting makes a significantly better variance structure!
221 # L= 383.7 (df=4, p<0.0001)
222 #No more Heteroscedasticity
223
224 # 5. Model Selection
225
226 lmeALL <- lme(fALL,
227              random=~1|PlotID/PatchID,
228              data=jena, method="ML", weights = varSpec)
229
230 #Important to choose the method "Maximum Likelihood" here because we are comparing models
    with different fixed effect structure. REML (default) is not possible.
231
232 # 5a. Global Model Selection by MiMiN
233
234 global.selection <- dredge(lmeALL, extra= alist(AIC))
235
236 global.selection[1:10] #only show the first 10 results
237
238 # 5b. Backward Selection
239
240 M1a <- update(lmeALL, .~. -I(Freq_Plot^2):Cover_Plot)
241 M1b <- update(lmeALL, .~. -I(Freq_Plot^3):Spec)
242 M1c <- update(lmeALL, .~. -Freq_Plot:SR_Plot)
243
244 anova(lmeALL,M1a,M1b,M1c) #M1a, Cover:Freq^2 removed
245
246 M2a <- update(M1a, .~. -I(Freq_Plot^3):Spec)
247 M2b <- update(M1a, .~. -Freq_Plot:SR_Plot)
248 M2c <- update(M1a, .~. -Freq_Plot:Cover_Plot)
249
250 anova(M1a,M2a,M2b,M2c) #M2c Freq_Plot:Cover_Plot removed
251
252 M3a <- update(M2c, .~. -Freq_Plot:Spec)
253 M3b <- update(M2c, .~. -I(Freq_Plot^2):Spec)
254 M3c <- update(M2c, .~. -I(Freq_Plot^3):Spec)
255 M3d <- update(M2c, .~. -Freq_Plot:SR_Plot)
256 M3e <- update(M2c, .~. -Cover_Plot)
257
258 anova(M2c,M3a,M3b,M3c,M3d,M3e) #M3e Cover_Plot removed
259
260 M4a <- update(M3e, .~. -Freq_Plot:Spec)
261 M4b <- update(M3e, .~. -I(Freq_Plot^2):Spec)
262 M4c <- update(M3e, .~. -I(Freq_Plot^3):Spec)
263 M4d <- update(M3e, .~. -Freq_Plot:SR_Plot)
264
265 anova(M3d,M4a,M4b,M4c,M4d) #M4d Freq_Plot:SR_Plot removed
266
267 M5a <- update(M4d, .~. -Freq_Plot:Spec)
268 M5b <- update(M4d, .~. -I(Freq_Plot^2):Spec)
269 M5c <- update(M4d, .~. -I(Freq_Plot^3):Spec)
270 M5d <- update(M4d, .~. -SR_Plot)

```

```

271
272 anova(M4d,M5a,M5b,M5c,M5d) # M5d SR_Plot removed
273
274 M6a <- update(M5d, .~. -Freq_Plot:Spec)
275 M6b <- update(M5d, .~. -I(Freq_Plot^2):Spec)
276 M6c <- update(M5d, .~. -I(Freq_Plot^3):Spec)
277
278 anova(M5d,M6a,M6b,M6c) # M5d stays the best
279
280 #Same result as global selection!
281
282 # 6. THE FINAL MODEL
283
284 fFinal <- formula(VR_spec~ Spec+
285                   Freq_Plot+
286                   I(Freq_Plot^2)+
287                   I(Freq_Plot^3)+
288                   Freq_Plot:Spec+
289                   I(Freq_Plot^2):Spec+
290                   I(Freq_Plot^3):Spec)
291
292 M.final <- lme(fFinal ,random=~1|PlotID/PatchID ,
293              data=jena , weights = varSpec)
294
295 M.final.ml <- lme(fFinal ,random=~1|PlotID/PatchID ,
296                data=jena , weights = varSpec , method="ML")
297
298 M.final.noweight <- lme(fFinal ,random=~1|PlotID/PatchID ,
299                       data=jena)
300
301 M.final.onerandom <- lme(fFinal ,~1|PlotID ,
302                       data=jena , weights = varSpec)
303
304 M.final.NOrandom <- gls(fFinal ,data=jena , weights = varSpec)
305
306 anova(M.final ,M.final.noweight)
307
308 #validating random effect structure:
309 AIC(M.final.NOrandom,M.final.onerandom,M.final)
310 #           df           AIC
311 #M.final.NOrandom 25 987.6298
312 #M.final.onerandom 26 989.6279
313 #M.final          27 983.6561
314
315 # 7. Model Validation Nr. 2
316
317 plot(M.final , main="Model Validation" , ylim=c(-3.5,3.5))
318 #looks ok
319
320 plot(M.final.noweight , main="Model Validation" , ylim=c(-6,6))
321 # weighting makes big difference
322
323 mean(resid(M.final)) #should be zero —> good
324
325 # 8. Summary & Interpretation
326
327 summary(M.final)
328 anova(M.final)
329
330 # numDF denDF F-value p-value
331 # (Intercept)      1   191 213.68824 <.0001
332 # Spec            4   191 141.13918 <.0001
333 # Freq_Plot       1   191 18.29208 <.0001
334 # I(Freq_Plot^2)  1   191  9.29896 0.0026
335 # I(Freq_Plot^3)  1   191  0.05521 0.8145
336 # Spec:Freq_Plot  4   191  5.20801 0.0005
337 # Spec:I(Freq_Plot^2) 4   191  3.43666 0.0097
338 # Spec:I(Freq_Plot^3) 4   191  3.41020 0.0101
339

```

```

340 #F-Values are high because the between-group variability in the species is high (attractive
      species vs. non-attractive species), high F-values are good
341
342 r.squaredGLMM(M.final.onerandom)
343 #R2m (marginal) : 0.5329026
344 #—> represents the variance explained by fixed factors
345 #R2c (conditional): 0.5341637
346 #—> both fixed and random factors (i.e. the entire model)
347
348 # 9. Plotting
349
350 Mlm <- glm(fFinal, data=jena)
351 sub <- list(jena.ger, jena.lat, jena.lot, jena.ono, jena.tp)
352 color <- c("cornflowerblue", "blue4", "maroon", "red", "orange")
353
354 par(mfrow=c(1,1))
355 plot(VR_spec~Freq_Plot, data=jena, xlim=c(0,100), type="n", ylab="Per-Flower Visitation
      Rate [Log-Scale]", xlab="Frequency [%]", main="Visitation Rate Depending on Frequency ",
      log="y")
356 legend("bottomright", legend = unique(jena$Spec), pch=20, col=color, cex=0.9, bg="white")
357 for (i in 1:5){
358   points(VR_spec~Freq_Plot, data=sub[[i]], col=color[i], pch=20, cex=.8)
359   xv <- data.frame(Freq_Plot = jena$Freq_Plot, Spec=species[i])
360   xv <- xv[order(xv$Freq_Plot),]
361   yv <- predict(Mlm, newdata=xv)
362   lines(xv$Freq_Plot, yv, col=color[i], lwd=1)
363 }
364
365 all.glm <- glm(VR_spec ~ Freq_Plot + I(Freq_Plot^2) + I(Freq_Plot^3), data=jena)
366 xv <- seq(min(jena$Freq_Plot), max(jena$Freq_Plot), 1)
367 yv <- predict(all.glm, newdata=data.frame(Freq_Plot=xv), se=TRUE)
368 polygon(x=c(xv, rev(xv)), y=c(yv$fit + 2 * yv$se.fit, rev(yv$fit - 2 * yv$se.fit)), col="#
      CDC9C960", border="#CDC9C940")
369 lines(xv, yv$fit, lwd=3, lty=2)

```

./jena.R

NetLogo Model

```

1 ; Agent-based Model of bees foraging on a meadow with two co-flowering plant species competing for the shared pollinator
2
3 ; Masterthesis of Helen Czioska
4 ; Faculty of Environment & Natural Resources at the Albert-Ludwigs-University Freiburg
5
6
7 breed [bees bee]
8 bees-own [
9   reward-memory ;string - momory for the amount of reward gained from each of the last 4 visits
10  species-memory ;string - remembers the species of the last X flowers
11  flower-memory ;string - memory of the location of the last 4 visited floweres
12  array ;array - vision of the bee-agent on the grid
13  choice ;boolean - gives the currently preferred flower (flower-constancy); changes with unsuccsessfull search and bad reward
14  change-prob ;float - propability to change the preferred flower type. Increases with low reward and unsuccsessfull search
15  flowers-visited ;integer - counter how many flowers this bee-agent already visited
16  flight-count ;integer - duration of unsuccsessfull search for the next preferred flower
17  change-count1 ;integer - how often does this pollinator switch preferences due to bad reward?
18  change-count2 ;integer - how often does this pollinator switch preferences due to unsuccsessfull search?
19  handling-time ;integer - time the bee-agent needs to extract all reward (handling time = reward * 4 + 0.5 + penalty)
20  change-penalty ;integer - bee-agent needs additional 3seconds to extract all reward when unexperienced
21  average-reward-count ; Integer - counter for foraging on flowers with average reward
22 ]
23
24
25 patches-own [
26   species ;boolean - defined species, does not change
27   reward ;float - reward (max 1)), emptied with every visit by a bee-agent and restored by the reward-function
28   visit-count ;integer - counter how often this flower was visited
29   pollination-count ;integer - counter for every successfull pollination
30 ]
31
32
33 globals[
34   flower-number ;integer - how many flowers are on the meadow
35   flower-number1 ;integer - how many flowers of species 1 are on the meadow
36   flower-number2 ;integer - how many flowers of species 2 are on the meadow
37   cluster-number1 ;integer - number of clusters of species 1
38   cluster-number2 ;integer - number of clusters of species 2
39 ]
40
41
42 .....
43 .....
44 to setup
45   clear-all
46
47   ; create a meadow with patches of flowers of two pollinator-dependent flower species
48
49   ask patches [set pcolor 64 set species 0] ;the grass
50
51   ;create n patches with a average size of cluster-degree flowers
52   set flower-number round ((flower-cover / 100) * (count patches))
53   set flower-number1 round (flower-number * (frequency / 100))
54   set flower-number2 round (flower-number - flower-number1)
55   set cluster-number1 (flower-number1 / cluster-degree)
56   set cluster-number2 (flower-number2 / cluster-degree)
57
58   if(flower-number1 > 0)
59   [ ifelse (cluster-number1 >= 1)
60     [ask n-of cluster-number1 patches with [species = 0] [set species 1 set pcolor 47 set reward 1 ]]
61     [ask n-of 1 patches with [pcolor = green] [set species 1 set pcolor 47 set reward 1 ]]
62   ]
63
64   if(flower-number2 > 0)
65   [
66     ifelse (cluster-number2 >= 1)
67       [ask n-of cluster-number2 patches with [species = 0] [set species 2 set pcolor 104 set reward 1 ]]
68       [ask n-of 1 patches with [pcolor = green] [set species 2 set pcolor 104 set reward 1 ]]

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69 ]
70
71 while [count patches with [species > 0] < flower-number ]
72 [ask one-of patches with [species > 0]
73 [
74   if (species = 1 and (count patches with [species = 1] < flower-number1))
75   [ifelse (any? patches with [species = 1 and any? neighbors with [species = 0]])
76     [if(any? neighbors with [species = 0])[ask one-of neighbors with [species = 0] [set species [species] of myself set pcolor
77       [pcolor] of myself set reward 1 ]]]
78     [ask n-of 1 patches with [pcolor = green] [set species 1 set pcolor 47 set reward 1 ]]
79   ]
80   if (species = 2 and (count patches with [species = 2] < flower-number2))
81   [ifelse (any? patches with [species = 2 and any? neighbors with [species = 0]])
82     [if(any? neighbors with [species = 0]) [ask one-of neighbors with [species = 0] [set species [species] of myself set pcolor
83       [pcolor] of myself set reward 1 ]]]
84     [ask n-of 1 patches with [pcolor = green] [set species 2 set pcolor 104 set reward 1 ]]
85   ]
86 ]
87
88
89
90 ; create the bee-agents
91
92 create-bees number-bees
93 [ ;set shape "bee" ;(Agents with an actual bee-shape)
94   set shape "circle" set color 26
95   setxy random-xcor random-ycor
96   set reward-memory (list)
97   set flower-memory (list)
98   set species-memory (list)
99   set flight-count 0
100   set flowers-visited 0
101   set handling-time 0
102   set change-penalty 3
103   let next-flower min-one-of patches with [species > 0 ][distance myself]
104   face next-flower set choice [species] of next-flower
105   ;bee-agents choose the closest flower to their starting point for initial preference
106 ]
107
108 reset-ticks
109
110 end
111
112
113 .....
114
115 to move
116
117   ifelse (flight-count < flightsteps-until-change)
118   [
119     ; find out if there are any flowers in the visible area of the bee which have the preferred species AND were not
120     ; visited before
121     set array patches in-cone view 180 with [(species = [choice] of myself) and (not member? self [flower-memory] of
122       myself) ]
123     let next-flower min-one-of array [distance myself]
124     ifelse any? array
125     [ face next-flower fd 1 ] ;face the nearest flower and move to it in a straight line (see Viswanathan 2008)
126     [ rt random-normal 0 stdev-angle fd 1 set flight-count flight-count + 1 ]
127   ]
128
129   [
130     set change-prob change-prob + 0.1 ; every second the bee-agent does not find a preferred flower, the
131     ; change-probability increases by 10% (see Chittke et al. 1997)
132     ifelse (random-float 1 < change-prob) ; if the random-number is below the change-prob, the bee-agent just
133     ; picks the next available flower regardless of its species

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133         set array patches in—cone view 180 with [ (species > 0) and (not member? self [flower—memory] of myself) ]
134         let next—flower min—one—of array [distance myself]
135         ifelse any? array
136             [ face next—flower fd 1 set choice [species] of next—flower set change—count2 change—count2 + 1 set
               change—prob 0]
137             [ rt random—normal 0 stdev—angle fd 1 set flight—count flight—count + 1 ]
138     ]
139     [ rt random—normal 0 stdev—angle fd 1 set flight—count flight—count + 1 ]
140 ]
141
142 end
143
144 .....
145
146 to visit
147
148     if (length (reward—memory) > 0) ; precaution for the first visit
149     [
150         if (reward < (mean reward—memory) / 2) [set change—prob change—prob + 0.1 set average—reward—count 0] ;bad reward:
            change—porpability increases
151         if (reward > (mean reward—memory) * 2) [set change—prob 0 set average—reward—count 0] ;very good reward:
            change—porpability decreases
152         if ((reward < (mean reward—memory) * 2) and (reward > (mean reward—memory) / 2)) [ set average—reward—count
            average—reward—count + 1]
153         if (average—reward—count > 5) [set change—prob 0 set average—reward—count 0] ; 5 times average reward:
            change—porpability decreases
154
155         ifelse (choice = 1)
156             [ if (random—float 1 < change—prob) [set choice 2 set change—prob 0 set change—count1 change—count1 + 1 set
              average—reward—count 0]]
157             [ if (random—float 1 < change—prob) [set choice 1 set change—prob 0 set change—count1 change—count1 + 1 set
              average—reward—count 0]]
158     ]
159
160     ;remember reward
161     while [(length reward—memory) >= 4] [ set reward—memory (but—last reward—memory) ]
162     set reward—memory (fput [reward] of patch—here reward—memory )
163
164     ;remember flower—location
165     ; Every pollinator has a memory for visited flowers. Pollinators avoid recently visited flowers (see Goulson1999 for review)
166     ; Goulson 2000: "Pollinators can remember the location of the last 4 visited flowers"
167     while [(length flower—memory) >= 4] [ set flower—memory (but—last flower—memory) ]
168     set flower—memory (fput patch—here flower—memory )
169
170
171     ;calculate handling—time
172     ; 4 s/J (Roubik 1989 in Kunin & Iwasa 1996)
173     ; 0.5s constant minimum handling time (see K&I 1996)
174     ; 3s Penalty for change of flower, "experience extract time" (see K&I 1996)
175
176     if (length (species—memory) > 0)
177     [ifelse (first species—memory = [species] of patch—here)
178         [set change—penalty 0]
179         [set change—penalty 3]
180     ]
181     set handling—time (round (reward * 4 + 0.5 + change—penalty))
182
183     if ( member? ([species] of patch—here) species—memory)
184     [set pollination—count pollination—count + 1]
185
186     while [(length species—memory) >= pollen—reach] [ set species—memory (but—last species—memory) ]
187     set species—memory (fput [species] of patch—here species—memory )
188
189     set flight—count 0
190     set flowers—visited flowers—visited + 1
191     set reward 0
192     set visit—count visit—count + 1
193
194 end
195

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196
197 .....
198
199 to stay
200
201 set handling-time handling-time - 1
202
203 end
204
205
206 .....
207
208
209 to go
210 ask bees [
211     ifelse (handling-time > 0)
212         [stay]
213         [ifelse (([choice] of self = species) and (not member? patch-here [flower-memory] of self))
214             [visit]
215             [move]
216         ]
217 ]
218
219 ask patches [if (reward < 1) [set reward reward + reward-function]] ; see Kunin & Iwasa 1996: Max. 1 J
220
221 tick
222
223 end
224
225
226 .....
227 to-report visits [spec]
228 report sum [visit-count] of patches with [species = spec]
229 end
230
231 to-report pollination-success [spec]
232 report sum [pollination-count] of patches with [species = spec]
233 end
234
235 to-report reward-report [spec]
236 report (mean [reward] of patches with [species = spec])
237 end
238
239 to-report count-change-flightsteps
240 report sum [change-count2] of bees
241 end
242
243 to-report count-change-reward
244 report sum [change-count1] of bees
245 end
246
247 to-report number-flowers [spec]
248 report count patches with [species = spec]
249 end

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./bee_final.txt

Erklärung

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